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PROBLEMS OF EVOLUTION AND PRESENT METHODS OF ATTACKING THEM[1]

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THE problems of evolution have been much the same from Darwin's day to this, but the present methods of attacking them are in many respects different from those which prevailed a generation ago. One great problem with which the earlier naturalists were concerned, viz., the fact of evolution, is by common consent, no longer a problem; if it has not been demonstrated that the living world arose through evolution, it has at least been rendered so probable that demonstration could add little to our certainty. And yet we should all like to see the demonstration of evolution on a large scale, such as must have been operative in the past history of living things, but we have little reason to hope that such a demonstration will soon be made.

The enduring problems of evolution concern the means or factors of transmutation. Here also the old method of attack, viz., observation and induction, led to no certainty but only to probabilities of a lower order than those which speak for the truth of evolution. For the past twenty years the futility of the old theories and discussions has been generally recognized, and the desire for more exact knowledge has been keenly felt. Consequently

[1] Introductory address in the annual discussion before the American Society of Naturalists, Princeton, N. J., December 28, 1911.

analytical and experimental work on the problem of the factors of evolution was begun some twenty years ago and has been continued with ever-increasing interest to the present time.

In the first enthusiasm over the experimental method of attack it seemed to many students of this problem that at last a path had been found which would lead straight to the goal, that the causes of all evolution were about to be revealed, and that the practical control of evolution, with all that this implies, was almost within reach. About that time a young physiologist said to the Director of the Zoological Station at Naples, "Why do you spend so much money publishing these beautiful monographs on the Fauna and Flora of the Gulf of Naples?" Dr. Dohrn replied, "You are the first person who has ever asked me such a question; many have asked *how* and *where* I got the money, but no one has asked *why*. What do you mean?" "Only this," said the physiologist, "that within twenty-five years we shall be making experimentally an indefinite number of faunas and floras, and the present one will then be only one of many." In the opinion of many investigators at that time, experimental evolution was soon to give us a new world of living things, and it was about to reveal conclusively the causes of evolution. We have now had one or two decades of this experimental evolution, and it may be worth while to inquire, What has been the net result? If the answer should seem to be somewhat discouraging I would beg to remind you that is so chiefly because the problems have been found to be much greater than was at first supposed. The experimental method as applied to the evolution problem has justified itself; it has set the problem in a clear light and it has brought forth facts of the greatest significance, but it has not enabled man to do in twenty-five years what it took nature twenty-five million years to do.

I

The most significant work on genetics since the time of Darwin is that which is identified with the name of

Mendel. According to the doctrine of Mendel and his followers each organism is composed of a multitude of unit characters, which do not blend nor lose their identity when mixed with others as a result of sexual reproduction, but which may be expected to come out in the end, practically as they went in at the beginning. This conclusion has modified in a striking manner the entire conception of evolution and heredity. We no longer discuss the origin of species, but rather the origin of characters; we no longer rely upon chance to bring out certain hereditary characters, but are enabled at will to make many analyses and syntheses of these characters. These discoveries probably mark the greatest advance ever made in the study of heredity; they have made it probable that evolution proceeds by the evolution of individual characters; but have they shed any light on the method and manner of this evolution? Permutations of Mendelian characters we may have without number, of new combinations of these there may be no end, but, so far as known, no new characters are formed by such temporary combinations, there is no "creative synthesis," no lasting change. Evolution depends upon the appearance of new characters; the discoveries of Mendel show us how to follow old characters through many combinations and through many generations, but they do not show us how new characters arise. These discoveries have given us an invaluable method of sorting and combining hereditary qualities, but Mendelian inheritance, as commonly expounded, does not furnish the materials for evolution.

Many modifications of Mendelian inheritance have been described, many alterations of dominance, or blending of characters, the causes of which are not yet well understood. Perhaps in these "unexplored remainders" may be found the causes of new characters. It is not yet certain that the unit characters, or rather their determiners in the germ, are beyond the reach of environmental influence; it is not certain that in their mixture with others they never combine or influence each other in such manner as to form new unit characters. Indeed, it is difficult

to understand how new characters could ever appear except under one or the other of these conditions. We particularly need at this time more knowledge of the mechanism underlying the gross phenomena of Mendelian inheritance, and then perhaps we may learn under what conditions this mechanism may be altered.

As a result of the work of Mendel and his followers we know much more about heredity than was known before, we have learned how to separate and to combine hereditary characters, we have learned to look for evolution in the appearance of new characters, but we have not learned how to produce new characters.

II

Practically all who have ever thought or written on evolution have found the principal causes of the transmutation of old characters into new ones in the action of extrinsic, or environmental, forces on the organism. As the result of years of labor on this subject Darwin concluded that "variability of every sort is due to changed conditions of life." It is well known that environmental changes produce many kinds of modifications in organisms, and in general these modifications are the more profound the earlier they occur in ontogeny; it is known that slight alterations of the germ cells may produce great modifications of adult structure, and it seems reasonable to suppose that environmental changes of the right sort applied to the germ cells at the right stage would lead to a permanent modification of the substance of heredity and hence to the appearance of new characters of evolutionary value. And yet one of the most striking results of recent work is to show the small effect of environmental changes of all sorts on racial characters. Marked individual modifications may be produced which do not become racial. Usually not one of thousands of variations which occur have any evolutionary value. These variations come with changing environment and with changing environment they disappear. Just as in the individual, so also in the race there seems to be a power

of regulation which causes a return to the type, when once this has been departed from.

In several instances recent investigators have found, or have thought they have found, experimental evidence of the inheritance of characters acquired through environmental changes. But these evidences are by no means conclusive. In a few cases it is known that the effects of changed environment last through two or three generations and then disappear. In such cases racial, or specific, regulation is slow; in most cases this regulation takes place in the first generation after the environmental change disappears. Perhaps in this lingering effect of a changed environment we have the first indication of the appearance and fixation of a new character. Here, undoubtedly, much work of value remains to be done.

Very rarely a sudden variation, or mutation, arises which is perpetuated by heredity and which forms the basis of a new race. In most cases which have been carefully studied such mutations consist in the dropping out of some old character rather than in the addition of a new one, but at least they represent modifications of the hereditary characters, and as such they furnish material for evolution. Whence and how they appear we do not know, for like the kingdom of heaven, they come without observation. Their infrequency, amidst the multitude of somatic variations, indicates the wonderful stability of racial types and teaches respect for Weismann's doctrine of a germplasm, relatively stable, independent and continuous.

This distinction between somatic and germinal variations, between those which concern only the individual and those which are inherited and furnish material for evolution, marks the greatest advance in the study of evolution since the work of Darwin. And just as these germinal variations are the only ones of importance in the process of evolution, so the question of their origin is the greatest evolutionary problem of the present day. How are such germinal variations produced? Do they occur as the result of extrinsic or of intrinsic causes? By

instinct we are all Lamarckians and are inclined to follow Darwin in ascribing variability of every sort, germinal as well as somatic, to changed conditions of life. But this is by no means a necessary conclusion. It is conceivable that germinal variations result from combinations of different germplasms, as Weismann supposed, that the determiners of Mendelian characters do not always preserve their individuality, but sometimes unite in such way as to modify the unit characters; but as yet we have no evidence that new characters are formed in this way, and the study of Mendelian inheritance has made this possibility less probable than it once was. Again it is possible that germinal variations, and new hereditary characters, may result from intrinsic changes in the germplasm, comparable to the spontaneous changes which occur in radium, for instance; such a view of transmutation through intrinsic, spontaneous, changes has points of resemblance to the doctrine of orthogenesis, but of its truth or falsity we have no sufficient evidence.

If changes in the germplasm may be induced by extrinsic conditions, then a real experimental evolution will be possible; if they can not be so induced we can only look on while the evolutionary processes proceed, selecting here and there a product which nature gives us, but unable to initiate or control these processes.

III

Darwin's theory that selection is the most important factor in preserving and building up evolutionary characters remains to this day a theory. The brilliant researches of our distinguished guest, Professor Johannsen, and of our President, Professor Jennings, have shown that the selection of fluctuations, or somatic variations, have no permanent effect in modifying a race; but selection or elimination of germinal variations may be an important factor in evolution, though it has little or nothing to do with the formation of new characters, and serves merely as a sieve, as De Vries has expressed it, to sort the characters which are supplied to it.

On the other hand, selection of favored races and elimination of the unfit is still the only natural explanation of fitness, of adaptation, in organisms. As a species-forming factor selection is probably of less importance than Darwin supposed; as a possible explanation of the wonderful adaptations which all living things exhibit it seems to be all important; but extensive experimental investigations of the causes of adaptation are greatly needed.

IV

The microscopic study of the germ cells during the past twenty-five years—their growth, maturation, union in fertilization, and their subsequent development—has furnished material of the greatest importance for the comprehension of the mechanism of heredity and evolution, and yet almost everything in this field remains to be done. The parts played by the different constituents of the cell in assimilation, regulation and heredity are still in doubt, and in spite of many alluring hypotheses we know practically nothing about the way in which hereditary characteristics arise from the germ. The study of the cellular basis of heredity has to a large extent been guided and influenced by our knowledge of the gross phenomena of heredity, and this must always be the case; but the brilliant discoveries of the last few years as to the cellular basis of sex show the great assistance which the study of cytology may render to the science of genetics. Many interesting experiments have been made upon the germ cells in the attempt to shift dominance, to modify inheritance, to create new characters; in a few instances it has been shown that certain modifications of the embryo or adult organism follow certain modifications of the germ, but in no instance has it been shown that such modifications are inherited and are consequently of evolutionary value.

Not merely the constitution of the germ and the ways in which this may be modified, but also the precise manner in which the structures of the germ become trans-

muted into the structures of the adult are evolutionary problems of the greatest importance. It is an amazing fact that the great problems of ontogeny—*viz.* the underlying causes and mechanism of differentiation—are to-day, after more than a century of scientific observation and experiment, almost as complete a mystery as ever. If we are as yet unable to determine the precise manner in which the structure of the germ evolves into the structure of the adult in the common, ever-present phenomena of reproduction, it is small wonder that we have been unable to determine in detail the way in which one race is transmuted into another.

In conclusion I think it must be admitted that the experimental study of genetics has been a little disappointing. We had supposed that organisms would be more tractable, more willing to evolve, than we find them. The older view that organisms were plastic and could be moulded "while you wait" now reminds one of the view of certain childless theorists, that children are plastic clay in the hands of parents or teachers; both of these views neglect the fact that the living organism, delicate and responsive beyond compare, is still wonderfully strong, stable and stubborn. So far as the factors of evolution are concerned experimental study has thus far been a weeding-out process, and at times it seems that nothing will be left.

The problems of evolution are as much problems to-day as they ever were, and though some of these problems may soon be solved, we may rest assured that there will always be *the* evolution problem. The path which we thought led straight to the goal has had to be retraced with much labor; the hilltop from which we confidently expected to see the spires of Eldorado has only served to show us how great are the difficulties before us. But this is the order of nature, the common experience of all search for truth, and we would not have it otherwise. "For to travel hopefully is a better thing than to arrive, and the true success is to labor."

LIGHT THROWN BY THE EXPERIMENTAL STUDY OF HEREDITY UPON THE FACTORS AND METHODS OF EVOLUTION[1]

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THE most important contribution of modern studies in heredity to the topic of evolution has been *a new formulation of the problem*. Until a decade ago the problem of organic evolution was regarded as synonymous with that of the *origin of species*. We were, however, not agreed as to the definition of species; on the contrary, we realized that our notion of the term was exceedingly hazy. And, doubtless, the reason why we made so little progress in getting at the methods of evolution was because of this bad formulation.

To-day all this is changed. We think less of the origin of species and more of characteristics; of their nature, their origin and their distribution. The concrete question of the origin of a given species has become broken up into the questions of the origin of its differential *characters*. Thus, the problem of the origin of man has been broken up into the problems of loss of the tail, of the hairy coat, of skin pigmentation, of melanic iris pigmentation, the acquisition of a more complicated brain structure, the reduction of the lower part of the face, the acquisition of the ability to learn to count and talk, to wear clothes, to be honest, truthful, regardful of the property rights of others, and to exercise self-control in the sex sphere. So long as we formulated our problem as the explanation of the "origin of the human species," as though the human species were an indivisible unit, so

[1] Read (with slight alterations) before the American Society of Naturalists at Princeton, December 28, 1911.

long we floundered helplessly in the quicksand of unclearness and complexity; now that we recognize our study to be the history of any inheritable trait we move on surer ground. And so, in general, progress is to be made in the future by careful attention to the evolution of characters.

The second change in the formulation of the problem that is due to the modern study of heredity is that we no longer consider even the character as the ultimate unit of evolution, but regard it rather as a product of such a unit. For the character is, in some way or another, determined by the conditions in or the constitution of the germ-plasm and these conditions and this constitution, though very different from the adult characters, are their germinal representatives; and these germinal representatives are the real units to be studied. Thus we do not to-day formulate our problem as the evolution of man, or of a blue-eyed man, but ask how the determiner for brown-eye became lost from the germ-plasm. So, in general, the problem of evolution is formulated as that of the history of the germinal determiners of characters.

Besides formulating more precisely the problem of evolution, modern studies have discovered certain methods of evolution which were not appreciated a decade ago. First, we have come to realize that, though not uniformly, yet to a surprising degree, characteristics are *independent* of one another and, hence, that their determiners in the germ-plasm are commonly not bound together. The evidence for this is found in the breeding experiments that have been performed on scores of species of animals and plants, both feral and domesticated. Breeders have taken advantage of this independence to create almost any desired combination of known characters. Thus, in poultry the single pea or rose comb may be combined with a black, white or game plumage, with or without unfeathered shanks. The shepherd's purse that grows by the roadside may be made with either of two forms of capsules combined with

four forms of leaf in the rosette stage; fruit-flies (*Drosophila*) may have any one of several colors of eye combined with either short or long wings, and so on. The characteristics that are associated in an individual are, for the most part, not necessarily associated. The group of characteristics that distinguishes individuals of one "species" from those of another is largely an accidental one; and it is, therefore, not surprising that we so often find individuals which in one, two or several characters differ from the conventional description of their species, and these have in the past caused great difficulty to the species maker.

The fact that most characteristics are not necessarily associated—that they may occur in various combinations —certainly accounts for the multiplicity of "varieties" in domesticated species; and for much of the variation in feral species. Moreover, it probably accounts for the presence of many "species" in a genus. I may repeat here what I wrote in 1909.

> Dr. Ezra Brainerd has shown how many wild "species" of *Viola* have arisen by hybridization, as may be proved by extracting from them combinations of characters that are found in the species that are undoubtedly ancestral to them. In such highly variable animals as *Helix nemoralis* and *Helix hortensis* it is very probable that individuals with dissimilar characters regularly mate in nature and transmit diverse combinations of characters to their progeny. Indeed, if one examines a table of species of a genus or of varieties of a species one is struck by the paucity of distinctive characters. The way in which species, as found in nature, are made up of different combinations of the same characters is illustrated by the following example, taken almost at random. Among the earwigs is the genus *Opisthocosmia*, of which the five species known from Sumatra alone may be considered. They differ, among other qualities, chiefly in the following characters (Bormans and Kraus, 1900):
>
> Size: *A*, large; *a*, small.
> Wing-scale: *B*, brown; *b*, yellow.
> Antennal joints: *C*, unlike in color; *c*, uniform.
> Forceps at base: *D*, separated; *d*, not separated.
> Edge of forceps: *E*, toothed; *e*, not toothed.
> Fourth and fifth abdominal segments: *F*, granular; *f*, not granular.

The combinations of these characters that are found are as follows:

Opisthocosmia	*ornata:*	*AbcDEF.*
	insignis:	*ABcDEf.*
	longipes:	*AbCDEf.*
	tenella:	*AbCdef.*
	minuscula:	*aBCDEf.*

Other species occur, in other countries, showing a different combination of characters, and there are characters not contained in this list, which is purposely reduced to a simple form; but the same principles apply generally.

The bearing upon evolution of the fact that species are varying combinations of relatively few characters is most important. Combined with the fact of hybridization it indicates that the main problem of evolution is that of the origin of specific characteristics. A character, once arisen in an individual, may become a part of any species with which that individual can hybridize. Given the successive origin of the characters *A, B, C, D, E, F,* in various individuals capable of intergenerating with the mass of the species, it is clear that such characters would in time become similarly combined on many individuals; and the similar individuals, taken together, would constitute a new species. The adjustment of the species would be perfected by the elimination of such combinations as were disadvantageous.

Second, modern studies have taught us that we have regarded the steps of progress in evolution in too crude a way. One school adhered to the view that characters, as we know them in the adult, arose gradually in phylogeny as in ontogeny, *i. e.*, that the germ-plasm undergoes a development as the child does. Another school proclaimed for discontinuity in phylogeny; *i. e.*, that the conditions in or the constitution of the germ-plasm undergoes from time to time more or less abrupt changes. Such abrupt changes are not altogether unknown in ontogeny; for the sundering of a chromosome or the perforation of a membrane involves essentially abrupt or discontinuous processes. The new era of experimental breeding is leading us to a position that is in some respects intermediate between the views of these two schools. We have discovered a hitherto unsuspected multiplicity of inheritable units, indicating a vaster complexity of the system of determiners in the germ-plasm

than we had dreamed. Sometimes a prominent character is represented by a single determiner like (perhaps) roseness of the comb of the fowl; but in most cases there is a multiplicity of factors, as in human hair and skin pigments, in the yellow of mice, in shank feathering of fowls and in seed coat-color of oats. In consequence of the fact of this multiplicity of factors and of the fact that a variable number may be present in different cases the adult character appears in numerous *grades* of development.

Indeed, the gradation of characters is, in these cases, such that one has to recognize that discontinuous variation passes over into continuous variation, in the sense that 40, 41, 42 form a continuous series, if not in the sense that x, $x + dx$, $x + 2dx$, etc., do. If a desire for uniformity leads us to conclude that all variations in the germ-plasm are discontinuous at least we see in many of these variations sufficient justification for the continuity hypothesis of the old-fashioned selectionist. The new light that has been thrown on the subject is the certainty of discontinuity in most cases and apparent continuity only in the limiting case. The reason why the old continuity hypothesis was for so long a time accepted was that we had underestimated the fineness and the multiplicity of the units of inheritance.

Third, experimental work has thrown a new light on the process of selection. It is clear that Darwin confused under this term two ideas that we now sharply separate; namely, the selection of the most favorable individuals and the selection of the most favorable blood, race, strain or pure line (biotype, Johannsen). In so far as not the soma but the germ-plasm is the proper basis of selection it is clear that the favorable biotype is what we should seek for to make most rapid advance. By this means Pearl has increased the fecundity of his poultry; thus, probably Castle has extended step by step the color pattern of rats; thus poultry fanciers have improved the color pattern of Barred Plymouth Rocks; thus I have gained a syndactyl race of fowl.

The method of personal selection has been widely used by the less philosophical breeders. I do not think it fair to Darwin to designate it as the exclusively Darwinian selection. Whether advance can be made by personal selection seems to me still an open question. Granting our inability to reason about genotypical constitution from the phænotypical, still, other things being equal, and in the long run and with great numbers of individuals an extremely high variant is more apt to belong to a genotype with a high mean than to one with a low or intermediate mean. Thus a breeder who selects merely the very best somas of a large number will be apt to select any superior biotype that may occur in his material. This is doubtless the reason why breeders who consider only the somas of their breeding stock nevertheless sometimes make progress; for they are occasionally fortunate enough to stumble upon a new biotype.

Fourth, the results of experiments have thrown light on the long-discussed question of the discontinuity between *species*, of the swamping effects of intercrossing new varieties with the parent species and the necessity for isolation to permit new varieties to become established as distinct species. We now realize that the danger of swamping which formerly seemed so logically necessary is, from our new point of view, not really to be seriously considered. Characters are rarely, if ever, swamped. Apparent swamping by intercrossing occurs when the new character depends on many determiners. But it is not, even in this case, really swamped; for no true blend occurs but, on the contrary, a segregation of the original extreme conditions takes place. This is well illustrated by the case of human skin color. When the germ cell that carries white skin color unites with the germ cell that carries black skin color the "white" character seems swamped in the offspring; but the swamping is only apparent. Two mulatto parents have children of various tints and, occasionally, one with a clear white skin, as well as one with a black skin like the original negro ancestor.

Neither white nor black is truly swamped. The extreme white or black conditions are rather rare, as is to be expected where a multiplicity of factors is involved. Thus, if there were two (2) factors P′, P″ involved in the negro skin then in F_2 one in sixteen should be negro-black, one in sixteen pure white, and half of the remainder should be light mulatto and half dark mulatto. Although studies on this subject are not sufficient to warrant exact quantitative conclusions, it is certain that more than two and probably more than three factors are involved in the pigmentation of the negro. If a number of mulattoes inhabited (as sole occupants) an oceanic island, and bred there, in the course of generations both the white and the black types of skin color would be found again—the two extreme types are not swamped. Consequently from our present point of view, isolation is much less essential than was formerly thought to be the case. Practically important as it may be to keep races pure and ensure the absence of intergrades or hybrids, it is not essential to the survival of new traits that have arisen in the midst of the old stock.

Fifth, the experimental study of heredity has thrown light upon the question of the origin of *new determiners*. Every critical experiment that has been tried demonstrates again that the somatic condition exercises little or no influence upon the determiners in the germ-plasm. The first crucial experiment on this subject of which I know was that of Francis Galton, who infused into "silver-gray" does the blood of either yellow, black and white, or common agouti rabbits. In one case an angora buck and yellow doe had their carotid arteries so connected that for over half an hour the blood of each flowed into the body of the other; so that about one half of the blood of each was alienized. Yet, when the rabbits that had been operated upon were used as parents, the offspring indicated that their germ-cells had undergone no modification in consequence of the foreign blood. Recently the question has been revived by Guthrie, who

made the experiment of engrafting foreign ovaries into foster mothers very unlike the original females whence they were taken. He concluded that the offspring were modified in such a way as to prove that the transplanted germ-plasm had received something from the foster mother. Unfortunately Guthrie erred here, as my repetition of his experiments showed. For unquestionably, the hens that were operated upon regenerated their proper ovaries and produced no eggs from the engrafted ovaries. Dr. Phillips, working with Castle, engrafted black-bearing eggs from one female guinea pig into albino guinea pigs and then mated the females that had been operated upon with an albino male. All offspring were entirely black, proving, first, that the engrafted ovaries were functional and, second, that the determiners of the engrafted germ-plasm were not modified by the soma of the albino mother. On the other hand, the experiments of Standfuss, Tower and Kammerer on animals and MacDougal on plants apparently indicate that under the influence of various conditions of moisture, temperature and chemical action the *germ-plasm* may be changed. These results, probable as they are, await confirmation. If fully confirmed they will afford a picture of one way in which new determiners may originate.

Finally, some light has been thrown by modern experimental studies on the subject of *adaptation*—for Darwin the corner stone of organic evolution. But here, it must be confessed, the contribution has not been great. That there is such a thing as selective elimination is plainer than ever. That some characteristics are compatible with the environment and some incompatible is incontestibly true. Two cases in poultry illustrate this. I have a lot of rumpless fowl; the cocks are sexually active and the hens lay numerous eggs; but every egg is sterile, for the reason that the erection of the tail feathers in the hen is essential to the clean exposure of the cloacal opening for the transfer of the sperm. Hence, since in the rumpless hens the cloacal opening is not accessible to the

sperm, such a sport must, in nature, be eliminated. Under domestication it is continued by trimming away the feathers that cover the vent. Similarly, winglessness in male fowl renders copulation difficult because the wings serve the cock as balancers while treading the hen. These then are examples of characteristics that must be eliminated in nature. In the case of certain striking colors in poultry there is evidence that they are selected against; their possession gives their owner a handicap.

On the other hand certain new characteristics of fowl may be preserved because apparently they offer no handicap. Thus in the rumpless fowl the oil gland is absent and the birds seem to be none the worse on that account; their plumage is bright and quite as resistant to a wetting as that of birds with an oil gland at the base of the tail. The striking fact that our experimental work yields is the great number of new characters that seem to bear no relation to fitness or unfitness, but are truly neutral. Thus I can not find that polydactylism, shank-feathering or its absence, and the lower grades of single, pea and rose comb have any adaptive significance for poultry. One can invent adaptive explanations for them or their absence in birds, but there is no reason for thinking that the explanations are significant. On the other hand, there is accumulating considerable experimental support for Darwin's theory of sexual selection; but of this it is early to speak. On the whole, I think it may be fairly said that experimental work supports the principle of selective elimination but finds many characters that are wholly neutral.

To sum up, modern experimental study of heredity has given a new formulation to the problem of evolution and has given definite data on the method of evolution. It formulates the problem of evolution as the problem of the nature and origin of the germinal determiners of characters. It has shown that, for the most part, the new determiners arise one at a time and are independent of one another, may occur in any combination and may be

transferred from one strain or species to another. It has been shown that the unit characters are much more numerous and finer things than we had thought and, therefore, that the steps of evolution are frequently very small ones and are taking place in many directions. It has shown the relative unimportance of the isolation factor, since true blends of characters rarely, if ever, occur. It has demonstrated the lack of influence by soma upon germ-plasm; but has rendered it probable that external conditions may directly modify the determiners of the germ-plasm. It brings support for the view of selective elimination of undesirable traits but finds that many, if not most, characters that arise are neutral in respect to any adaptive significance. Finally, it looks forward with a justifiable expectancy to the completer experimental test of the factors of evolution and their eventual complete elucidation.

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BIOTYPES AND PHYLOGENY

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[THE substance of this paper was presented to the American Society of Naturalists at the Princeton meeting under the title "Pure Lines and Phylogeny." Dr. Johannsen entered an emphatic protest against the use of "pure line" in the sense of a group of individuals characterized by an identical combination of the same determinants. Subsequent conversation with Dr. Johannsen, and the recent clear exposition by Shull (*Science,* Jan. 5, 1912, pp. 27–29) satisfied me that what I had considered "pure lines" (such as those distinguished by Jennings in *Paramœcium*) are the pure strains called biotypes by Johannsen. I have modified my paper accordingly and have avoided using the term "pure line." I have also abandoned the very convenient term "phenotype" because my use of it as a contrast to biotype is not strictly in accord with Johannsen's usage of it as a contrast to "genotype." At Princeton, I protested against Johannsen's use of the word genotype, because the word is preëmpted for a totally different usage. I suggested a substitute, but this failed to meet with Dr. Johannsen's approval. Since I have seen Shull's definition of "genotype" (to which Dr. Johannsen himself referred me), I think the objection to the word is greater than before because "type" implies a single definite thing or model and Johannsen's "genotype" is not that but is "the fundamental hereditary . . . combination of genes of an organism." In other words it is not a concrete thing but the intangible character of that thing. It seems to me the termination "plast" (πλαστός, moulded, formed, *i. e.,* formed from

the genes) expresses the idea better than "type" (τύπος, a figure, impression, model) and "genoplast" is quite as euphonious as "genotype." The adjective form is equally satisfactory, while the use of this term will not require the abandonment of "gene." In the following pages therefore I have used "genoplast" and "genoplastic" in place of genotype and genotypical and I do not believe any misunderstanding will be possible. I have no desire to insist on these words, however. The whole matter is a very trivial one and I would very much prefer that Dr. Johannsen should himself choose a substitute for "genotype." I can not, however, agree with him that genetics and systematic zoology are so far apart that no confusion can result from using identical terms in totally different senses. I believe that so far as possible workers in any branch of biology ought to keep in touch with as much of the whole field as may be possible, and that we should all endeavor to avoid ambiguity and unintelligibility in the use of such technical terms as are necessary.—H. L. C.]

Systematic zoology and botany deal primarily with species and varieties, and can not therefore be expected to throw light upon the existence of genoplastic groups. Indeed, only those systematists who deal with organisms which reproduce asexually or parthenogenetically are likely to have any personal contact with them or even to meet with direct evidence for or against their occurrence. Since, however, the existence of such pure strains (biotypes) seems to have been definitely proved[1] the question of their relationship to the phylogenetic problems with which the systematist has to deal becomes one of some interest.

The problems of phylogeny are those of complicated polygenoplastic groups—so complicated indeed that the most complex of chemical compounds is simple in comparison. The study of these problems makes for caution

[1] JENNINGS, H. S., 1911, AMERICAN NATURALIST, Vol. 45, pp. 79–89.

in affirming that any one theory or hypothesis contains all the truth. Thus we are coming to realize that neither the Darwinian nor the De Vriesian theory of the nature of the material upon which selection works is altogether complete in itself and that neither when properly understood wholly debars the other. If we accept the current Mendelian and genoplast theories of heredity, must we not admit that all variation is fundamentally discontinuous and that what has been called continuity is not really such? It may be convenient to use such terms as "continuity" and "discontinuity" but are they not subjective ideas rather than objective realities of importance? So, too, is it necessary to claim that the genoplast theory of heredity contains all the truth and that the transmission or "phenotype" theory is wholly false? It is easy to see how in pure line breeding "ancestral influence" is, as Johannsen says, "a mystical expression for a fiction" but in the complicated polygenoplastic groups of the higher Metazoa it is hard to see why the history of the formation of a gamete may not be of importance. Is this not virtually admitted by Johannsen when he grants the existence of "perturbations by infection or contamination"? And if this be granted, why is there any necessary antagonism between the genoplast theory of heredity and the belief that "discrete particles of the chromosomes" may be "bearers of special parts of the whole inheritance"?

However this may be, none of us has any doubt that the discovery of biotypes has been a real stimulus to experimental work, and there is no reason why it may not also be a stimulus to the investigation of phylogenetic problems even though it does not assist greatly in their immediate solution. Among the difficulties of the systematist perhaps none is better known than that which we may call *the problem of large genera*—genera made up of dozens, in some cases indeed of hundreds, of species, many of which are poorly defined and more or less intergrading. Some of these genera, as *Cratægus, Unio* and

Salmo, have become notorious and are not infrequently referred to as proof of the futility of systematic work. Does the discovery of biotypes afford any help in explaining the existence of such genera?

I think that it does, particularly when considered in connection with the broadest interpretation of Mendel's law. If we compare one of these inclusive genera with one which contains few and well-defined species, we see that the essential difference lies in the latter having the characters sharply defined, with little diversity and no blending, while in the former the same or similar characters show so much diversity and such a tendency to blend that the resulting recombinations are most perplexing. It has occurred to me that we have here a condition of affairs analogous to what we find in the development of the individual. Certain individuals with unlike parents show what seems to be a blending of the parental characters, while in numerous other cases the characters of the individual can be referred unhesitatingly to one or the other parent. Thus, as the well-known investigations of Castle have shown, if lop-eared rabbits are crossed with rabbits having ordinary ears, the character of the ears in the offspring can not be referred to one parent rather than to the other, while if pigmented and albino rabbits are crossed, the color-character of the offspring in succeeding generations can be so referred without difficulty. This difference has been interpreted by Davenport and others as due to the potencies of the determinants, the apparent blending being associated with equipotency or an approach thereto, while the distinct characters result from allelopotency. Now may it not be that a similar inequality of potency occurs among the biotypes which go to make up a species? And so when reproduction takes place we find some species in which well-defined characters are dominant and the resulting individuals form easily recognized groups, while in other species there is a lack of definiteness and a blend-

ing of characters which make the resulting forms most confusing.

Jennings has shown that there are inherent difficulties, which have so far been prohibitive, in securing crosses between biotypes of *Paramœcium* under experimental conditions, yet it is obvious that such crossing must occur constantly in nature; otherwise the whole genoplast theory becomes reduced to an absurdity. Granting then the natural crossing of biotypes, let us consider the case of a species, which for simplicity's sake we will suppose is made up of three biotypes (1, 2 and 3), each of which is distinguished by certain character-combinations, designated *a, b* and *c,* respectively. If the union of 1 and 2 is readily effected, while that of 1 and 3 or that of 2 and 3 rarely occurs, it is evident that *ab* will far more commonly characterize the species than *ac* or *bc* which will indeed seldom appear. The species will therefore approach identity with one of its biotypes, which may thus be considered the dominant strain. The inequipotency of the biotypes and the resulting definiteness of character in the species are obvious. If, however, the union of 1 and 3, and of 2 and 3 are as readily effected as that of 1 and 2, *ac* and *bc* will occur as frequently in the species as *ab*. In such a case the biotypes are equipotent and the resulting species may be correspondingly ill-defined.

The hypothesis here suggested of the "*inequipotency of biotypes*" may thus be the explanation of the existence of the well-defined species so generally known, while the occurrence of large heterogeneous assemblages of either species or varieties may be interpreted as due to an unusual equipotency. The experimental determination of the existence of this hypothetical difference in the potency of the biotypes within a species would well be worth while, if it should ever prove to be possible. The study of large heterogeneous groups may suggest some other lines of investigation into the nature and even the origin of biotypes. For example, such groups occur chiefly, if

not wholly, in the more specialized portion of any stock and in some cases at least appear to be associated with the fading-out or senescence of that particular branch. This suggests the possibility that the potency of a biotype ultimately alters, even though there is no visible or tangible evidence of change.

A second problem which puzzles the systematist is the *variability in the value of a character* for distinguishing species, genera and even higher groups. Color is a familiar example of this. It is of real value among birds and in numerous other cases, but is almost worthless among many invertebrates. Does the knowledge of the existence of biotypes help us to understand why this is? At first thought one might say that here again the inequipotency of the biotypes was the explanation of the phenomenon, but further consideration will show that this is not the case, for of course the potency of a biotype will involve all of its characteristic determinants and not merely that or those associated with the character in question. It is clear then that the value of any character for distinguishing species from each other—in other words, its value for systematic work—depends on the actual determinants in the genoplastic groups composing those species. The variability in systematic value shown by a given character is due then, not to the potency, but to *the composition of the biotypes* involved. Thus if all the biotypes contain identical color determinants, then color will be an absolutely constant character in that species, but the greater the diversity in the color determinants of the biotypes the more variable will the color of the species be and the less useful the color be as a distinguishing character. Conversely, we may say that the value of color in systematic work will depend on the degree of identity in color-determinants among the biotypes composing the species concerned. If this is so, the study of systematic characters and the measuring of their diversity may suggest some characteristics of biotypes as yet unsuspected. Thus biometrical work

even in a polygenoplastic population receives an added indorsement.

A third problem of the systematist (and for this occasion the last) is found in the fact that *diversity of morphological characters in any given species is not haphazard* or indiscriminate, but is generally restricted to such definite lines as to indicate more or less distinct stages in the phylogenesis of that species. The belief that diversity is significant and that its meaning may be discovered has received extraordinary confirmation in Jackson's just published, magnificent monograph on Echini[2] in which the subject is very fully discussed. An illustration taken from his work will help to make clear the desired point. In any regular sea-urchin, such as *Arbacia* or *Strongylocentrotus*, a group of ten plates surrounds the periproct, five of which are radial in position and are called oculars while the other five are interradial and are called genitals. Now in some echini all of these ten plates are in contact with the periproct and thus form a simple continuous ring but in most of the Recent species, the oculars are much smaller than the genitals and some or all of them are separated from the periproct by the meeting of adjoining genitals. In other words, some of the oculars may be excluded from the periproct and such are said to be *exsert*, while those which separate adjoining genitals and reach the periproct are called *insert*. Now Jackson has demonstrated conclusively, contrary to the widely held belief that the insertness of oculars is a matter of age and size, that for each species of sea-urchin there is a characteristic arrangement of the genito-ocular ring and that this arrangement is oftentimes a very constant character. Thus in 2,100 *Arbacias* from Woods Hole, 87 per cent. have all the oculars exsert and in more than 20,000 *Strongylocentroti* from Maine 95 per cent. have the two posterior oculars insert.

Having demonstrated the constancy of this character, Jackson has gone on to an analysis of the variations from

[2] Jackson, R. T., 1912. *Mem. Boston Soc. Nat. Hist.*, Vol. VII.

the normal arrangement, occurring in large series of adult specimens. And he has clearly shown that these variations are nearly always significant. There are 32 possible arrangements of the plates of the genito-ocular ring and there is no mechanical or structural reason why any one of them should not occur. If variation were perfectly haphazard every one would occur and there is no obvious reason why they might not occur, with equal frequency. Yet in fifty thousand specimens examined by Jackson, representing 137 different species of Mesozoic and Recent Echini, ten of these possible arrangements *never* occurred, and of the remaining 22 fourteen are so rare that altogether they aggregated less than 1½ per cent. of the specimens. As a very large proportion of these were individuals abnormal in some other particular, it is fair to say that of 32 possible arrangements of the genital and ocular plates only eight (or at most ten) occur normally. Even more striking are the following facts:

When only a single ocular plate is insert, it is one of the posterior pair; this is the case in 99⅓ per cent. of the specimens having one ocular insert.

When two oculars are insert, they are the posterior pair in more than 99 per cent. of the cases and in *every* case one of them belongs to that pair.

When three oculars are insert, they are the two posterior and usually the left, but sometimes the right anterior; this is demonstrated by almost 99 per cent. of the cases.

When four oculars are insert, the one exsert is invariably either the mid-anterior or right anterior.

These figures show how surprisingly definite variation is in a character which, so far as we can see, might vary with equal ease in any one of 32 ways. Yet it is only when we examine a particular case that the significance of this definiteness appears.

Jackson's work is full of such cases, but as most of us are familiar with *Strongylocentrotus,* we will consider an illustration from that genus, which, in the old, broad

sense, accepted by Jackson, includes more than twenty species. Of these some have the ambulacra relatively simple, the compound plates being made up of only four or five elements each, while in the more specialized species there may be as many as ten elements in each compound plate. The various species can be arranged roughly in a series beginning with the simplest and ending with the most specialized[3] and Jackson shows that the species with the simplest ambulacra (*S. lividus*) has "no oculars insert" as the species character, with "right posterior ocular insert" as a common variant, while those with the most complex ambulacra (*S. franciscanus* and *purpuratus*) have two and often three oculars insert. Now in our common *Strongylocentrotus* from Maine, while practically 95 per cent. have two oculars insert, nearly 3 per cent. have only one insert, as in the common variant of *S. lividus*, while about 2 per cent. have three insert as in the usual variants of *S. purpuratus*. Jackson calls these *arrested* and *progressive* variants, respectively, according to whether they resemble a more simple or a more complex allied species. Whether the terminology be accepted or not, the significance of such facts can not be ignored. Are we any better prepared, with our present knowledge of the existence of biotypes, to understand the reason for this significance of variation?

If we compare a polygenoplastic group with a highly complex chemical compound, an analogy is suggested which warrants our answering this question affirmatively. In building up such a compound synthetically, the specific properties of the constituents result in the formation of certain definite compounds. These substances are necessary for the further combinations without which the ultimate compound could not be formed. In other words, the formation of the desired product is possible only because the chemical reactions

[3] There are some interesting exceptions, but as they do not affect the subsequent argument, they need not be discussed here.

will take place in an orderly sequence, in consequence of the fixed specific properties of the elements involved. Now any existing species of plant or animal is a similar union of diverse elements and the possibilities of its development would seem to be limited by the same conditions which limit the formation of the chemical compound, namely, the nature of the elements and the orderly sequence of the reactions. (In either case external conditions, the environment, would make a profound difference, but for simplicity's sake we may omit reference to that influence.) As long as one believes that the elements composing a species are potentially variable in all directions, it is evident that only the pressure of external conditions can prevent an indefinite and unmeaning variety in the product. Such a belief results in making natural selection through the environment the supreme directive agent in evolutionary progress, and really puts more responsibility upon that important factor than it can reasonably be expected to bear. But as soon as it is shown that the elements involved are persistently unchanging to a remarkable degree, it becomes clear that an orderly sequence in their successive interactions will follow just as in the formation of a chemical compound. Now biotypes are the biological elements which enter into the formation of a species, and the discovery of their existence and apparent persistency makes the existence of an orderly sequence in development quite comprehensible and indicates clearly why diversity is so rarely haphazard. As in the chemical synthesis, used as an illustration, the final reaction follows necessary antecedent reactions, so in the development of the species the last step necessarily depends on the preceding, and the evolution of a group is therefore bound to be strictly linear and in definite directions. Now just as in a chemical synthesis without adding to or subtracting from its original constituent elements the process may be stopped, altered or accelerated, either by addition or removal of some substance or by

change in the external conditions, so the process of development of a species or of any of its component individuals may be arrested, altered or accelerated by similar means. Thus variants arise, individual or racial, sometimes slight, sometimes marked, but necessarily within the limits laid down by the specific properties of the biotypes involved. This may be well illustrated by one of Jackson's discoveries about variation in the genito-ocular ring of the common tropical sea-urchin, *Tripneustes*. In specimens from Florida and the West Indies, 36 per cent. have only the two posterior oculars insert, 38 per cent. have three (the left anterior plus the posterior) and 18 per cent. have four (right and left anterior plus the posterior). Evidently then individual variants both arrested and progressive are common but within very restricted limits. Further than this it appears that in Bermuda a racial variant can be distinguished, for in specimens from that locality 61 per cent. have only two oculars insert, 35 per cent. have three and only 2 per cent have four. Now it matters not at all whether the Bermuda race is considered an arrested variant or the West Indian form a progressive variant; the important fact is the evidently marked but definitely limited racial diversity. The study of such variants, however little light it may throw on the immediate cause of their appearance, is bound to help make clear the normal line of development of the species to which they belong, and emphasizes the definiteness and the significance of their diversity. But if biotypes are really the fixed and unchanging elements which compose a species, the problem as to why this diversity is so commonly definite and significant is apparently simplified not a little by our knowledge of their existence.

It is unnecessary to suggest any other phylogenetic problems and the bearing of the study of genetics on them, for if in these which I have suggested it has not been shown that such study is helping us to understand these problems better and is even indicating solutions,

multiplication of such cases will not help the matter. Personally, I believe that the experimental work now so extensively carried on in the study of genetics is throwing a flood of light on all biological questions and that systematists not only may but must make use of the demonstrated results of such study, in attacking their own special problems, if they are really in earnest in the purpose to solve them.

SHORTER ARTICLES AND DISCUSSION

A LITERARY NOTE ON MENDEL'S LAW

THE ever-increasing extension of the doctrine of Mendelism brings it year by year to the attention of a widening circle of general readers. Its application in the field of eugenics has aroused a popular desire for a further knowledge of the now famous principles of Mendel. Owing to the relative inaccessibility of Mendel's original publication the exact terms in which he formulated his conclusions have not been readily available. To meet in some measure this lack of ready reference the following brief, synoptic statement of the fundamental principles of Mendel is here presented in his own words, together with certain collateral notes that may be of value to students of this important law.

The general term "Mendel's Law" is usually applied to several complex principles discovered by Gregor Mendel while studying inheritance in certain plant hybrids. Various other designations, however, appear in the literature, *e. g.*, Mendel's "Law of Heredity,"[1] "Law of Inheritance,"[2] "Laws of Alternative Inheritance,"[3] and "Law of Varietal Hybrids."[4] These principles were enunciated by Mendel in a paper entitled, *"Versuche über Pflanzenhybriden"* ("Researches on Plant Hybrids"), which appeared in the *Verhandlungen der naturforschenden Vereines in Brünn,* Vol. 4, 1865, *Abhandlungen,* pp. 3–47,[5] but escaped the attention of biologists until the year 1900, when by De Vries,[6] Correns[7] and von Tschermak,[8] they

[1] Castle, W. E., *Proceedings American Academy of Arts and Sciences,* Vol. 38, 1903, p. 535.

[2] Biffin, R. H., *Journal Agricultural Science,* Vol. 1, 1905, p. 1.

[3] Weldon, W. F. R., *Biometrika,* Vol. 1, 1901, p. 228.

[4] De Vries, H., "Species and Varieties," Chicago, 1905, p. 716.

[5] Reprinted in *Flora,* Vol. 89, 1901, pp. 364–403.

[6] De Vries, H., "Das Spaltungsgesetz der Bastarde," *Berichte der deutschen botanischen Gesellschaft,* Vol. 18, 1900, pp. 83–90.

[7] Correns, C., "G. Mendels Regel über das Verhalten der Nachkommenschaft der Rassenbastarde," *Berichte der deutschen botanischen Gesellschaft,* Vol. 18, 1900, pp. 158–168.

were independently and almost simultaneously rediscovered.[9]

Mendel's principles have been rephrased by later writers, and they are now usually referred to as the Law of Dominance, the Law of Segregation, and the Law of Recombination, respectively.

I. THE LAW OF DOMINANCE[10]

This so-called law is derived from the following principle of Mendel ("Versuche," etc., pp. 10–11):

In der weiteren Besprechung werden jene Merkmale, welche ganz oder fast unverändert in die Hybride-Verbindung übergehen, somit selbst die Hybriden-Merkmale repräsentiren, als *dominierende*, und jene, welche in der Verbindung latent werden, als *recessive* bezeichnet.

Translated this principle reads:

Those characters which pass entirely or almost entirely unchanged into the hybrid combination and consequently in themselves represent the characters of the hybrid, are designated as *dominant*, and those which become latent in the combination are termed *recessive*.

Since dominance is rarely absolute this principle is not general and should not be termed a law; indeed Mendel did not claim it as a law. Recent statements of the "Law of Dominance" may be thus summarized:

When the two parents differ in respect of two contrasted characters, only one, the dominant character, will appear in the hybrid. Dominance, however, is seldom perfect, so that the dominant character in a hybrid seldom reaches as full expression as in the dominant parent.

II. THE LAW OF SEGREGATION.

Mendel's second principle ("Versuche," etc., p. 17) is thus stated:

[8] Von Tschermak, E., "Ueber künstliche Kreuzung bei *Pisum sativum*," *Zeitschrift für das landwirtschaftliche Versuchswesen in Oesterreich*, Vol. 3, 1900, pp. 465–555.

[9] De Vries's paper was received for publication on March 14, 1900, and that of Correns on April 24, 1900. Tschermak, in a postscript to his communication, says: "Die gleichzeitige Entdeckung Mendels durch Correns, de Vries (*Berichte der deutschen botanischen Gesellschaft*, 1900) und mich erscheint mir besonders erfreulich."

[10] "Man hat dieses die 'Prävalenz-Regel' genannt," Correns, C., "Uber Vererbungsgesetze," *Verhandlungen der Gesellschaft deutscher Naturforscher und Ärzte*, 77 Versammlung, 1905, Part I, Leipzig 1906, p. 207.

Da die Glieder der ersten Generation unmittelbar aus den Samen der Hybriden hervorgehen, wird es nun ersichtlich, dass die Hybriden je zweier differirender Merkmale Samen bilden, von denen die eine Hälfte wieder die Hybridform entwickelt, während die andere Pflanzen gibt, welche constant bleiben, und zu gleichen Theilen den dominirenden und recessiven Character erhalten.

This may be translated as follows:

Since the members of the first generation[11] arise directly from the seeds of the hybrids, it is now evident that hybrids, for each pair of differentiating characters, form seeds, one half of which develops again the hybrid form, while the other half produces plants which remain constant and in equal proportions receive the dominant and recessive characters.

Various terms have been applied to this law by different authors, *e. g.*, "Law of Disjunction,"[12] "Law of Purity of Germ Cells,"[13] "Law of Separation of Characters in Crosses,"[14] and "Law of Dichotomy."[15] Generalized, the law may be stated in the following form:

In self-fertilized species an individual which is a hybrid with reference to a particular pair of characters tends to produce progeny one fourth of which is of pure race like one of the parents of the hybrid, another fourth of pure race like the other parent, while the remaining half is hybrid, like the original hybrid itself,"[16] that is, "from the inbred heterozygote come dominants and recessives in the proportion of 3:1, and only one dominant in three is pure, the other two being heterozygote.[17]

The above statement is purely objective;[18] it states the results

[11] This is the F_2 generation of current literature.

[12] De Vries, H., *Comptes rendus de l'académie des sciences*, Paris, Vol. 130, 1900, pp. 845–847.

[13] Castle, W. E., *Proceedings American Academy of Arts and Sciences*, Vol. 38, 1903, p. 537.

[14] De Vries, H., *Journal Royal Horticultural Society*, Vol. 25, 1901, p. 243.

[15] Davenport, C. B., *Biological Bulletin*, Vol. 2, 1901, p. 307.

[16] Spillman, W. J., "Application of Some of the Principles of Heredity to Plant Breeding," Bulletin No. 165, Bureau of Plant Industry, U. S. Dept. Agriculture, 1909, p. 9.

[17] Punnett, R. C., "Mendelism." Cambridge, 1907, p. 23.

[18] For this paragraph and the one immediately following, the writer is indebted to Professor W. J. Spillman.

of a cause, but gives no hint of that cause. It is not strange, therefore, that the modern statement of this law should have gravitated backward toward the fundamental cause underlying the law. The more usual statement of it at the present time is an inference from the facts observed, and may be stated as follows:

When an individual is heterozygous for a given character it produces two kinds of gametes with reference to that character, one like those of one of its parents and the other like those of the other parent.

Mendel himself gives the corresponding statement of the law of recombination; that is, he states the inference about the kinds of gametes a hybrid must produce, as inferred by the types of the resulting progeny.

The principle of segregation, closely approximated long prior to Mendel both by Goss[19] and by Sageret,[20] was clearly enunciated by Naudin,[21] but these writers did not formulate their

[19] "In the summer of 1820, I deprived some blossoms of the *Prolific blue* of their stamens, and the next day applied the pollen of a *dwarf Pea*, and of which impregnation I obtained three pods of seeds. In the following spring, when these were opened, in order to sow the seed, I found, to my surprise, that the colour of the Peas, instead of being a deep blue, like their female parent was of a *yellowish white*, like the male. Towards the end of the summer I was equally surprised to find that these white seeds had produced some pods with all blue, some with all white, and many with both blue and white Peas in the same pod.

"Last spring, I separated all the blue Peas from the white, and sowed each colour in separate rows; and I now find that the blue produce only blue, while the white seeds yield some pods with all white, and some with both blue and white Peas intermixed."—Goss, John, "On the Variation in the Colour of Peas, occasioned by Cross Impregnation." In a letter to the Secretary. Read October 15, 1822. *Transactions of the Horticultural Society of London*, Vol. 5, 1824, pp. 234–235.

[20] "Ainsi donc, en définitive il m'a paru qu'en général la ressemblance de l'hybride à ses deux ascendans consistait, non dans une fusion intime des divers caractèrs propres à chacun d'eux en particulier, mais bien plutôt dans une distribution, soit égale, soit inégale, de ces mêmes caractères: je dis égale ou inégale, parce qu'elle est bien loin d'être la même dans tous les individus hybrides provenant d'un même origine, et il y a entre eux, une très grande diversité."—Sageret, A., "Considérations sur la production des hybrides, des variantes et des variétés, en général, et sur celles de la famille des Cucurbitacées en particulier." *Annales des sciences naturelles*, Vol. 8, 1826, p. 302.

[21] "Tous ces faits vont s'expliquer naturellement par la disjonction de deux essences specifiques dans le pollen et les ovules de l'hybride."

results in terms of numerical ratios as did Mendel. Knight[22] and Gärtner[23] as well as Wichura,[24] Godron[25] and Vilmorin[26]

"Supposons, dans la Linaire hybride (*L. vulgaris* × *L. purpurea*) de première génération, que la disjonction se soit faite à la fois dans l'anthere et dans le contenu de l'ovaire; que des grains de pollen appartiennent totalement à l'espèce du père, d'autres totalement a l'espèce de la mère; que dans d'autres grains la disjonction soit nulle ou seulement commencée; admettons encore que les ovules soient, au même degré, disjoints dans le sens du père et dans le sens de la mère; qu'arriverat-il lorsque les tubes polliniques descendront dans l'ovaire et vont chercher les ovules pour les féconder? Si le tube d'un grain de pollen, revenue à l'espèce du père, recontre un ovule disjoint dans le même sens, il se produira une fécondation parfaitement légitime, dont le resultat sera une plante entièrement retournée à l'espèce paternelle."

Naudin, Ch., "Nouvelles recherches sur l'hybridité dans les végétaux," *Nouvelles archives du muséum d'histoire naturelle de Paris*, Vol. 1, 1865, pp. 150, 153.

[22] "Blossoms of a small white garden pea, in which the males had previously been destroyed, were impregnated with the farina of a large clay-coloured kind with purple blossoms. The produce of the seeds thus obtained were of a dark gray colour, but these having no fixed habits, were soon changed by cultivation into a numerous variety of a very large and extremely luxuriant white ones, which were not only much larger and more productive than the original white one, but the number of seeds in each pod were increased from seven to eight, to eight or nine, and not unfrequently, in one variety to ten. The newly made gray kinds I found were easily made white again by impregnating their blossoms with the farina of another white kind. In this experiment some of the seeds in the same pod would produce gray, and others white offspring, as occurs frequently in animals, which bring many young ones at birth, when the breeds of the male and female are of different colours."

Knight, T. A., "A Treatise on the Culture of the Apple and Pear, and on the Manufacture of Cider and Perry." Ludlow, 1801, pp. 37–38, footnote.

[23] "Het allerduidelijkst evenwel is de invloed van het vreemde stuifmeel op de eitjes in dit opzigt bij de *Leguminosen*, wanneer b. v. de stempel van *Pisum sativum luteum* met het stuifmeel van *Pisum sativum viride* bestoven wordt, zoo ontstaan in deszelfs peulen zaadkorrels welke aan die der moeder gelijk zijn, doch andere van eene groene en nog andere van eene gevlekte, dat is, van eene groene en gele kleur. Deze zaadkorrels uit de eerste voortteling, zoowel de groene als de gele en de gevlkte, geven in de tweede voortteling peulen, die hetzelfde verschil, als die uit de eerste voortteling, opleveren."

Gärtner, C. F., "Beantwoording der Prysvraag over bastardeering," *Natuurkundige Verhandelingen van de Hollandsche Maatschappy der Wetenschappen te Haarlem*, Vol. 24, 1838, p. 52.

[24] Wichura, Max, "Die Basterdbefruchtung im Pflanzenreich, erläutert an den Bastarden der Weiden," Breslau, 1865.

also seem to have come very near to the discovery of Mendel's principles.

III. THE LAW OF RECOMBINATION[27]

This law is based upon the following Mendelian principle ("Versuche," etc., p. 22):

> Die Nachkommen der Hybriden, in welchen mehrere wesentlich verschiedene Merkmale vereinigt sind, stellen die Glieder einer Combinationsreihe vor, in welchen die Entwicklungsreihen für je zwei differirende Merkmale verbunden sind.

This principle may be thus translated:

> The progeny of hybrids, in which several essentially different characters are combined represent the terms of a series of combinations, in which the development series for each pair of differentiating characters are united.

Spillman in his recent paper entitled "The Application of Some of the Principles of Heredity to Plant Breeding,"[28] thus concisely states this law:

> In the second generation of a hybrid there tends to occur every possible combination of the original parent characters.

This law was also discovered by Spillman independently in 1901 and announced provisionally by him in a paper read before the Association of American Agricultural College and Experiment Stations in November of that year.[29]

The clearest and most comprehensive account of Mendel's work extant is probably that of Bateson[30] in which may be found a full discussion of the doctrine of Mendelism together with a translation in English of Mendel's original papers. The French

[25] Godron, D. A., "De l'espèce et des races dans les êtres organisés," 2d ed., Vol. 1, Paris, 1872, pp. 180–266.

[26] Vilmorin, H., "Note sur une expérience relative à l'étude de l'hérédité dans les végétaux," Paris, 1879, pp. 1–11. Extrait des mémoires de la société nationale d'agriculture de France—Année 1877.

[27] "Gesetz der Selbständigkeit der Merkmale," Correns, *l. c.*, p. 208.

[28] Bulletin No. 165, Bureau of Plant Industry, U. S. Dept. Agriculture, 1909, p. 22.

[29] Bulletin No. 115, Office of Experiment Stations, U. S. Dept. Agriculture, 1902, p. 88.

[30] Bateson, W., "Mendel's Principles of Heredity," Cambridge, 1909.

translation by Chappellier,[31] and also the recent works by Baur,[32] Haecker,[33] and Goldschmidt,[34] will be found very useful to the general student of Mendelism.

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THE RANGE OF SIZE IN THE VERTEBRATES

A SMALL shrew, *Microsorex winnemana,* recently described from Virginia by Preble, is said, if conclusions from but two specimens may be drawn, to be the smallest species of shrew and therefore the smallest mammal yet known from America.[1] These specimens measured 78 and 86 mm., respectively, in total length. *Microsorex hoyi* (Baird) of the eastern and central states averages from 82 to 88 mm. and *Sorex fontinalis* Hollister and *Sorex personatus* Geoffroy are but slightly larger. *Blarina parva* (Say) a short-tailed shrew, averaging in total length about 75 to 80 mm., is in this respect smaller than *M. winnemana,* but much larger in breadth, cranial and other characters. The smallest existing mammal is probably a minute *Crocidura* of the subgenus *Pachyura* from Madagascar.

The Insectivora, essentially an archaic and primitive group, reached its highest development in point of numerous and diverse adaptations in the Middle Eocene, from which there has been a gradual and steady decline. *Sorex* is known from the Middle Oligocene, *Talpa,* the mole from the Upper Oligocene and *Erinaceus,* the hedgehog from the Lower Miocene. These are some of the oldest of existing genera of mammals. The Malayan genus *Gymnura,* an Erinaceid, was said by Huxley[2] to possess the most generalized structure of all placental mammals. The persistence of the group is without doubt due in a large part to the small size and relative inconspicuousness of its members.

[31] Chappellier, A., "Recherches sur des hybrides végétaux (Traduction française). *Bulletin Scientifique de la France et de la Belgique,* Vol. 41, 1907, pp. 371–420.

[32] Baur, E., "Einführung in die experimentelle Vererbungslehre," Berlin, 1911.

[33] Haecker, V., "Allgemeine Vererbungslehre," Braunschweig, 1911.

[34] Goldschmidt, R., "Einführung in die Vererbungswissenschaft." Leipzig, 1911.

[1] *Proc. Biol. Soc. Wash.,* Vol. 23, p. 101, 1910.

[2] *Proc. Zool. Soc. London,* p. 657, 1880.

The separation of Madagascar from Africa has permitted the continuance of the relatively large Centetidæ, the tenrecs, of which *Ericulus, Centetes* and *Hemicentetes* have developed a spiny coat and *Limnogale* has become aquatic. Similarly, the rare and interesting Zalambdodont, *Solenodon,* has been able to continue an existence by isolation in Cuba and Hayti. Even thus isolated, *Solenodon,* judging from its extreme rarity, barely maintains a foothold. The aberrant Tupaiidæ, or Oriental tree shrews, are, as indicated by their name, arboreal and the African Macroscelididæ, or elephant shrews seek refuge by leaping and by skulking. The South African Chrysochloridæ, or golden moles, and the familiar Talpidæ are subterranean. A subterranean habitat implies a restricted stature. *Erinaceus,* the well-known hedgehog, and the African *Potamogale,* the only relatively large non-insular insectivores, are well protected, the former by its spiny coat and the latter by its aquatic habits. The Soricidæ containing the smallest members of the order are largely nocturnal. During the long stretch of time since the Eocene culmination of the group and the gradual evolution of more modern mammalia, the Insectivora have become extinct with the exception of those especially protected, insular, subterranean or of insignificant size. Smallness here seems an attendant trait of archaism. The earliest American mammals, the Triassic Protodonts, *Dromatherium* and *Microconodon* and among recent mammals certain Murine rodents closely simulate this diminutive stature.

The massive Rorqual whale, *Balænoptera sibbaldii* Gray, of the North Atlantic, sometimes reaching a length of eighty-five feet, is the bulkiest vertebrate which has ever existed. The Cetacea are likewise a primitive and probably degenerate group. Other aquatic mammals, such as the Sirenia, Pinnipedia, etc., similarly reach immense proportions, due, very likely, to the lack of a compensatory element in the environment. The tallness of the giraffe, which is an adaptation to arboreal grazing, produced by an elongation of the cervical vertebræ, coordinated of course with limb structure, has independently arisen in at least one other family. The giraffe-camels of the genera *Oxydactylus* and *Alticamelus,* respectively, of the American Oligocene and Miocene, parallel the existing giraffes.

The smallest known bird is *Calypte helenæ* (Gundlach) of

Cuba, measuring in total length but 57 mm.[3] Several other humming birds, notably *Mellisuga minima* (65 mm.) of Jamaica, are but slightly larger. The Trochilidæ comprise about 600 known forms, most of which are excessively small. *Patagona gigas* of the higher Andes, the largest of the group measures about 215 mm. in length. The size of the members of this family is an adaptation to the physical requirements of a highly active life, which is essentially that of securing food while hovering before blossoms. The Nectariniidæ or sun-birds of the Ethiopian and Indian Regions parallel the Trochilidæ in size and brilliancy. The Dicæidæ or "Flower-peckers" of India and Australia, and the Troglodytidæ and Regulidæ, wrens and kinglets of this country, likewise contain very small forms.

Sphærodactylus sputator Gray (45 mm. plus), occurring in the West Indies, is one of the very smallest of American reptiles.[4] *S. notatus* Baird (50 mm.) of Florida and the West Indies and a number of other West Indian lizards are hardly larger. The largest of existing lizards are members of the Varanidæ of Africa, Asia and Australia, the Malayan *Varanus salvator* (Gray) reaches a length of eight feet. Of the adaptive radiations which the Lacertilians have undergone, that branch containing the Amphisbænidæ, minute, legless, burrowing forms of tropical America and Africa, is of peculiar interest. This family presents a most remarkable illustration of the principle of heterology of Cope, of parallelism and convergence of other authors. Through the dominance of essentially similar environmental factors, certain species have come to resemble the earthworm with such fidelity, that the very chickens which follow the plow are said to seem unable to differentiate and indiscriminately pick them up.[5]

These remarks may apply equally well to the Typhlopidæ and Glauconiidæ, still widely distributed in tropical countries, archaic and degenerate, sightless, burrowing snakes, relicts of a once cosmopolitan assemblage, which contain the very smallest known Ophidians. *Helminthophis petersi* Boulenger (110 mm.) of Ecuador, *Typhlops anchietæ* Bocage (119 mm.) of Angola, Africa, *Glauconia dissimilis* (Bocage) (104 mm.) of the White Nile and *Glauconia bilineata* (Schlegel) (110 mm.) of the West

[3] Ridgway, *Rep. U. S. Nat. Mus.*, 1890, p. 295 (1892).
[4] Boulenger, "Cat. Lizards Brit. Mus.," 2d ed., Vol. 1, p. 219, 1885.
[5] Eigenmann, *Biol. Bull.*, Vol. 8, no. 2, p. 60, 1905.

Indies, are some of the smallest species. The largest existing reptile is the Ganges crocodile, *Gavialis gangeticus* (Gmelin) of northern India, which is said to attain a length of thirty feet or more. This, however, is insignificant in comparison with that attained by the sauropodous dinosaurs of the Mesozoic. The American genera *Atlantosaurus, Brontosaurus, Camarasaurus* and *Diplodocus* were immense creatures. *Atlantosaurus immanis* Marsh of the Wyoming Upper Jurassic, supposedly terrestrial from mechanical considerations, is one of the largest land vertebrates which has ever existed, probably upwards of one hundred feet in length. The uncompensated extravagance of energy in the maintenance of such immensity, coupled with the small and primitive brain, were without doubt to a great extent factors in the extinction of these gigantic vertebrates. These animals are without living descendants.

The familiar "spring peeper," *Hyla pickeringii* (Storer), about 20–28 mm., of eastern North America is the smallest American *Hyla* and thus one of our smallest batrachians. The Hylidæ, comprising about 150 species, have a practically cosmopolitan distribution with the exception of Africa and the Malay Archipelago. Essentially arboreal, in the dense, steaming tropical forests of South America they attain the highest diversity of generic and specific types. *H. pickeringii* does not ordinarily ascend into the trees until early in autumn. A number of true frogs are as small or smaller, thus *Arthroleptis sechellensis* Boettger of the Seychelles, interesting from its habit of carrying its eight or nine tadpoles affixed by their ventral surfaces to its back, is but about 20 mm. in length of head and body. The smallest salamander of the eastern United States is the red-back, *Plethodon cinereus erythronotus* Green, an elongate form of about 75 mm. The largest salamander and the largest existing batrachian is *Megalobatrachus japonicus* (Temminck), the giant salamander of Japan, which reaches a length of over five feet. At no time have the Batrachia been the dominant type of vertebrate life, either in size or variety of forms.

It is among the fishes that we find the smallest known vertebrates. Thus, *Mistichthys luzonensis* H. M. Smith,[6] an extraordinarily minute goby from Lake Buhi, Luzon, P. I., is accorded this distinction. The average length of this species is 12.9 mm. The average for egg-bearing females which exceeds the average

[6] *Science*, N. S., Vol. 15, p. 30, Jan. 3, 1902.

for males by one millimeter is 13.5 mm., the maximum is 15 mm., and the minimum is under 12 mm. This species is said to be a food fish of considerable importance as it is seined by the natives in large quantities, dried in cakes or mixed with spices, and is eagerly sought for. The great majority of the six hundred known species of Gobiidæ are less than 75 mm. in length. *Philypnus dormitor* (Lacépède) of Central America and the West Indies, the largest of the family, reaches a length of 600 mm.

The Etheostominæ or darters contain some of the smallest spiny-rayed fishes. *Microperca punctulata* Putnam (25–38 mm.) of the Central States is next to *Elassoma evergladei* Jordan (20–33 mm.) a minute percoidean of our southeastern swamps, the smallest American spiny-rayed fish and a number of other darters are but slightly larger. *Heterandria formosa* Agassiz, a diminutive viviparous Pœciliid, occurring in swamps and ditches from South Carolina to Florida, was for a long while considered the least of American vertebrates. This species has an average length of 19 mm. for males and 25 mm. for females. *Acanthophacelus bifurcus* of the ponds and creeks of British Guiana, recently described by Eigenmann,[7] is still smaller; the average for both sexes is 21.5 mm. and the largest of 74 specimens is 29 mm. long. A number of pregnant females are but 20 mm. in total length and one of these, preserved in alcohol, in the Indiana University collections weighs but .076 gram. The weight of living specimens is probably somewhat greater. The exact measurements of this specimen (I. U. No. 11,765) are as follows: total length 20 mm., length to base of caudal 16 mm., depth 5 mm. and breadth or thickness 3 mm. The smallest male specimen here, one in full nuptial coloration, measures 19 mm. over all. In all probability, the smallest new world vertebrate is *Heterandria minor* Garman,[8] from Villa Bella, Brazil. The average total length of this species is 18 mm. for males and 20.5 mm. for females. Females of but 19 mm. "contain fully developed embryos." With this may be contrasted the bulk of *Arapaima gigas* (Cuvier) of neighboring streams of Brazil and Guiana, said to reach a length of fifteen feet and to be the largest strictly fresh-water fish known.

[7] *Annals Carnegie Museum*, Vol. 6, p. 52, 1909.

[8] *Memoirs Mus. Comp. Zool.*, Vol. 19, no. 1, p. 92, 1895.

The Pœciliidæ or killifishes, found in most warm portions of the globe, comprise about two hundred very small species, the largest *Fundulus, Anableps,* etc., seldom exceed 300 mm. In the inviting streams of Central America where the majority of species occur, adaptive radiation, as in every large family of fishes, has taken place, from the central type *Fundulus,* resulting in the depressed catfish-like *Rivulus,* the beaked garpike-like *Belonesox,* the sunfish-like *Goodea,* the carp-like *Cyprinodon,* etc.

The origin of these small forms may probably be explained by the selective migration and the successive adaptation of the species occupying the deeper reaches of the streams. The Pœciliidæ usually feed at the surface and thus may tend to disseminate throughout the full extent of the shallower waters. *Acanthophacelus* has evidently been derived from *Pœcilia,* from which it differs chiefly in the acquirement of two rows of retrorse hooklets on the modified anal fin of the male, while *Heterandria* is of a different type with conical, carnivorous dentition and shortened alimentary tract. Further exploration may reveal still smaller species of these interesting little fishes, which are likely, however, to pass unobserved by all but the trained naturalist.

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NOTES AND LITERATURE

HEREDITY

F. E. Lutz contributes a very interesting paper[8] in which he presents evidence bearing on the effect of selection in a "pure" strain. Amongst wild flies of this species (*Drosophila ampelophila*) about one third of one per cent. present abnormalities in wing venation. By selection and inbreeding he was able to produce strains with practically 100 per cent. abnormality. In a good many crosses the abnormal venation behaved as a Mendelian recessive in which dominance of normal was not perfect. But in other cases the phenomena observed departed widely from the typical Mendelian behavior. The author suggests that the abnormality is due to a factor which has high fluctuating variability, and that these fluctuations are to a certain extent inherited. It is shown that Galton's law of ancestral inheritance does not apply to individual families, even when these are large (100 to 200 individuals).

If we knew the real cause of this abnormality we might possibly be able to reason about its peculiar behavior with some hope of elucidating it. Any attempt at explanation must necessarily be largely hypothetical. The writer would suggest that most of Lutz's data point to the presence of two factors for abnormality, one much stronger than the other, and one or both of them highly variable (fluctuating variability). Davenport found such a case (two factors, one stronger than the other). for the hood in certain fowls.[9] The writer has often thought there ought to be cases of Mendelian factors which just barely give rise to visible expression in the soma. Since all characters exhibit fluctuating variability, such a factor should behave much as the character which Lutz studied.

Lutz concludes that he has produced effects by selection in "pure lines." This is much to be doubted. The results he secured by selection fit very well the curves shown in my paper on "Some of the Principles of Heredity Applied to Plant Breeding"[10] for

[8] "Experiments with *Drosophila Ampelophila* Concerning Evolution," F. E. Lutz, Carnegie Institution of Wash., 1911.

[9] *Proc. Wash. Acad. Sci.*, "Lecture on Heredity," by C. B. Davenport.

[10] Bulletin Bureau of Plant Industry, No. 165.

selection in dihybrids. Lutz's results seem to be further complicated by the fact, to which he calls attention, that the great variability of the character in question gave apparent normals that were really abnormals genetically, and this very fact rendered the establishment of really pure lines a matter of great difficulty, if indeed not an impossibility. A line is not necessarily pure (genetically) because it has descended through many generations of the closest possible inbreeding from a single original pair. It is only pure in a Mendelian sense when all its allelomorphs are duplex and the members of each pair of them are identical in character. An individual might be pure in this sense even though both its parents were complexly bred mongrels. On the other hand, if Lutz's original pair were not thus pure, their descendants would only by chance constitute a pure line. It is very doubtful if Lutz has really proved the effect of selection in modifying a pure line, for it is not established that he worked with a pure line, in the sense in which that term is now used.

Professor E. B. Wilson has recently published an excellent review of cytological investigations relating to sex inheritance.[11] There appears now to be no doubt of the relation of sex to certain chromosomes in diœcious organisms. This relation is also interpretable from the Mendelian viewpoint, so that we may say that sex inheritance belongs in the category of Mendelian phenomena. In nearly all organisms thus far studied the female is to be regarded as homozygous and the male heterozygous for sex. Hence the male produces two kinds of spermatozoa, while the females produce only one kind of egg. When an egg is fertilized by the one type of spermatozoa the zygote is a female; if by the other, the zygote is a male. In general, the female diploid nuclei contain two of the sex chromosomes or two groups of them when the sex chromatin element is compound. The nuclei of the male contain only one of these elements, with or without a synaptic mate different from it in character. In sea urchins it has been shown that it is the female that is heterozygous. But in this case the female possesses one of the sex elements and the male none. In both cases the female is characterized by an excess in the number of the sex elements as compared with the male.

A large number of ordinary Mendelian characters have been

[11] "The Sex Chromosomes," *Arch. f. Mikrosko. Anat.*, Bd. 77, 1911, pp. 249–271.

shown to be sex limited in inheritance in such a manner that it seems certain they are in some way connected either with the sex-determining chromatic element or with the synaptic mate of this element (in the heterozygous sex). This links these characters with the chromosomes, and further strengthens the chromosome theory of Mendelian inheritance.

The writer is fully aware of the danger, in dealing with statistical data, of drawing conclusions from insufficient data or from data that have not been submitted to a full mathematical analysis, such as the determination of means, norms, standard deviations, and coefficients of correlation. Although I have no very full or accurate data on the subject and have not actually determined statistically the coefficients of correlation between the characters about to be mentioned, I am of opinion, after more or less superficial observation extending now over nearly half a century, that there is a noticeable degree of correlation between positiveness of statement, and inaccuracy of statement. An illustration of this correlation will be found in a paper by Dr. J. Arthur Harris, published in the November (1911) number of this journal. It is now fairly well established that the norms of a group of related genotypes can, in some cases at least, be arranged in a frequency curve. In my review of de Vries's "The Mutation Theory"[12] I cite this fact *to show that the type of variation represented by these genotypes comes under the head of what de Vries there defines as "continuous variation,"* as opposed to the "discontinuous variation," in which the norms of the variants can not be thus arranged. In Dr. Harris's paper he represents me as having cited the fact that these genotype norms form a frequency curve as a *proof of the genotype hypothesis.* I have not been able to find the time to look up other similar citations in this paper to see whether the same inaccuracy applies to them. The type of correlation we are considering is further illustrated in this paper in Dr. Harris's definition of genotype, from which he omits the word "homozygous." The definition is further inaccurate in including clonal varieties under the definition of genotype. The author of the term genotype, in a recent lecture in this city, defined it as "the descendants of a single homozygous individual propagated by self-fertilization."[13]

[12] AMER. NAT., Dec., 1910.

[13] Since the above was written it has been pointed out by several writers that the word genotype should be replaced, in the above sense, by "biotype" or "pure line."

THE DISTRIBUTION OF PLANTS IN NORTH AMERICA

A COMPREHENSIVE account of the phytogeography of North America has long been a desideratum, and it will be welcome news to botanists that this need has at last been filled. The work of Dr. Harshberger,[1] just issued, is an imposing volume, which will be quite indispensable to all students of plant distribution, and evidently represents an enormous amount of labor on the part of the author. A fair criticism that might be made is that it perhaps is too comprehensive. The book in the writer's opinion could have been very considerably reduced in volume without lessening its value, by drastic cutting of the first three parts, which are really introductory, and yet take up nearly half the book. The really essential facts concerning the geology, geography and climatology of North America could certainly have been presented in much less space. There is much needless repetition, and the arrangement of the topics is at times very confusing.

In addition to Dr. Harshberger's own work there is a summary of the book, sixty-three pages in extent, written in German by the editor of the series, Professor O. Drude.

It is the fourth section of Dr. Harshberger's book which will undoubtedly be of most value to the average botanical student. This deals with the North American phytogeographical regions, formations and associations, and comprises an account of the floras not only of the whole North American continent, but of the West Indies as well.

Nearly one hundred pages are devoted to the history of work published on the floras of various parts of North America, the bibliography alone comprising forty-six pages. This makes up Part One of the work. The second part—Geographic, Climatic and Floristic Survey—occupies seventy-seven pages. In this section are given very much in detail an immense body of facts, many of which could have been omitted without materially lessening the value of the summary. Nevertheless it contains very much that the student will find exceedingly useful.

This section makes very clear the great range of conditions on the North American continent, which explains the richness and variety of its flora. Very full statistics are given in this chap-

[1] "Phytogeographic Survey of North America," John W. Harshberger, "Die Vegetation der Erde," Vol. XIII.

ter, including many tables, temperature, rainfall, etc. From the eternal ice and snow of Greenland to the equatorial conditions on the Isthmus of Panama, practically the whole gamut of climate depending upon latitude is covered. Moreover, the great variety in topography in North America results in precipitations ranging from practically nothing in the extreme deserts of the arid southwestern United States and Mexico, to a rainfall of two hundred inches or more in some tropical regions like parts of Jamaica.

The presence of lofty mountains permitting a rich Alpine flora in the northwestern parts of the United States and Canada, is also an interesting feature of the vegetation of North America. In his division of the phytogeographical regions Harshberger recognizes four main divisions: Northern, Central, Southern and West Indian. The United States lies almost entirely within the second of these, only the region of the Great Lakes and a small area in the Gulf region encroaching respectively upon the northern and southern zones. The natural phytogeographical areas, however, are by no means determined by latitude alone, this being especially the case in the central zone, where there are several quite unrelated floristic regions lying in practically the same latitude. Such, for example, are the eastern forest area and the western Cordilleran region.

The pronounced continental climate of the great plains, with its yearly range of temperature from arctic cold to tropic heat, may be contrasted with the uniform mild climate of the Pacific Coast, where longitude plays quite as important a rôle in determining the distribution of plants as does latitude. For example, Victoria in latitude 48 has a mean temperature for January of 41.9° F., while St. Louis, almost 10° further south, is 12 degrees colder. This illustrates the differences in the conditions between the Pacific Coast region and the pronounced continental climate of the Middle West.

The southern area, including Mexico and Central America, is for the most part tropical in its climate, except for the temperate uplands of Mexico. Within the United States, Florida and the southernmost tier of states adjacent to Mexico, really belong to the southern area rather than to the central one.

In the third part of his volume Dr. Harshberger treats at great length the geologic history of North America, and its bearing upon the origin and distribution of the present flora. In

the course of this section he expounds his own views as to the origin of the North American flora, and the factors which have brought about its present distribution. While this section contains much important and interesting material, it can not be said that its arrangement is all that could be desired. After a perusal of the 174 pages contained in it, there is left in one's mind a very confused impression of a conglomeration of geology, phytogeography, and the origin of floras, together with other more or less disconnected topics. A large part of this section deals again with the phytogeographical areas already discussed at length in the previous section, and repeated in the fourth part of the book, but deals with them from the standpoint of centers of distribution rather than merely from latitude. It is to be regretted that the subject of the phytogeographical areas has not been treated as a connected whole, and also materially reduced, so as to bring out the salient points, instead of presenting a mass of details of very varying importance.

While, as might be expected, the plants treated are for the most part the flowering plants, still the lower plants are not entirely neglected, the Algæ especially coming in for a fuller treatment than is usually accorded them in works on plant distribution.

As the flowering plants, especially Angiosperms, are the predominant plants of the existing land floras, the geological history of the country before the Cretaceous is of relatively small importance as bearing upon the distribution of the existing vegetation, since it is not until the Cretaceous, or at the earliest the Sub-Cretaceous is reached, that recognizable remains of Angiosperms are met with. Professor Harshberger gives an excellent account, with maps, of the distribution of land and water areas during the Cretaceous and their significance as affecting the future distribution of North American plants.

During the lower Cretaceous a solid land mass occupied approximately the present area of North America, but was separated from South America by a wide gap through what is now Central America, allowing free communication between the Atlantic and the Pacific. At that time also there was still a broad land connection with Western Europe. Throughout the northern area both of the old and new world, it is evident that a very uniform vegetation flourished, with Conifers as the predominant trees.

During the later Cretaceous extensive changes took place. The great western mountain chains were thrown up and communication with South America was established; but there was a complete separation of the eastern and western land masses. A broad body of water extended without interruption from the Arctic Ocean to the Gulf of Mexico, and the whole of the great plains region to the east of the Rocky Mountains was then submerged. Professor Harshberger believes that this was the period which determined the separation of the Eastern and Western coniferous floras, and the foundation of the great differences in the general floral characters of Atlantic and Pacific North America.

The Cretaceous is notable in the history of the vegetable kingdom as the time when the highest types of plants first appeared, or at any rate when they are first recognizable. There are no certain evidences of Angiosperms previous to the Sub-Cretaceous. Apparently the Cretaceous was a period of great development of new plant forms, perhaps conditioned by the great changes in the physical character of the continent, these changes undoubtedly causing great changes of climate as well. Harshberger thinks that the Cretaceous was probably characterized by periods of mutation—used in the sense of De Vries. Whatever may have been the reason, during the Cretaceous most of the modern angiospermous types, and many of the living genera appeared. The great feature of the later Cretaceous and Tertiary forests was the preponderance of dicotyledonous trees and shrubs whose remains are found in great numbers. It is certain that many existing herbaceous genera must also have been present, but with rare exceptions these have not been preserved as recognizable fossils, no doubt owing to their perishable tissues which were not fitted to leave fossil remains except under exceptionally favorable conditions.

The high northern extension of the Cretaceous and Tertiary forests, especially in the Miocene, shown by the fossil deposits as far north as Greenland and Spitzbergen, indicates a relatively warm climate for these higher latitudes of the northern hemisphere. Moreover this northern forest belt seems to have been much the same throughout the whole extent of the northern hemisphere, very many species occurring both in the eastern and western hemisphere. Many of the most characteristic of the Miocene genera still exist in America, especially in the great

deciduous forest region of the southern Appalachians. Among the widespread Miocene genera which still exist in America may be mentioned Magnolia, Liriodendron, Vitis, Sassafras, Aralia, Nyssa. Indeed it is supposed that some of the Miocene species still survive. Among these are the southern Cypress (*Taxodium distichum*), Balsam Poplar (*Populus balsamifera*), Sweet Gum (*Liquidambar styraciflua*), Black Walnut (*Juglans nigra*) and many others.

With the redistribution of the forest flora due to the glacial epoch, many of these types disappeared from western America and Europe but have survived in eastern America and eastern Asia. It is clear also that genera now confined to the Old World also existed at that time in North America. A long list of the Cretaceous and Tertiary genera of North America shows, for example such extra-American genera as Banksia (Australia), Casuarina (Australia and Malaysia), Encephalartos (South Africa), Eucalyptus (Australia), Ginkgo (China), Hedera (Europe, Asia), Sterculia (tropics of the Old World and Australasia).

During Tertiary times the eastern and western parts of the continent were again united, and there seems to have been a fairly uniform northern flora throughout the Atlantic and Pacific regions, although the separation of the Atlantic and Pacific floras was already indicated, the difference in climate no doubt being influenced by the changes in elevation caused by the uplifting of the great western mountain masses, inducing a drier climate in the interior of the continent. It seems probable that to the north of the great forest belt extending across the continent was an arctic flora, remnants of which are found in the Alpine regions of the higher mountains where they presumably took refuge after the migrations subsequent to the great glacial epoch.

It is pretty generally agreed that the present distribution of plants in America is mainly the result of the advance of the great glacial sheet from the north. In the southward retreat of the great forest belt there was a division which, it has been suggested, was caused by the presence of the dry plains of the interior, which were unfitted for forest growth, and thus acted as a wedge separating the western forest, predominantly of coniferous trees, from the eastern forest mainly deciduous in character. Whether or not this is the true explanation, the fact

remains that at present the western forest is composed in the main of a great variety of coniferous trees adapted to dry summer conditions, while the eastern forest is distinguished by its great richness in deciduous trees adapted to a humid summer climate. Close to the retreating line of the forests, there presumably followed a belt of arctic vegetation clinging to the edge of the advancing glaciers.

With the retreat of the glaciers the plants advanced northward again, and the present distribution was finally established. Owing to the much greater altitude of the western mountains, it is especially upon these that we find a true Alpine flora, the more or less changed remnants of the arctic vegetation forced southward by the advancing ice sheet. It is true that a few arctic plants, like the Greenland sandwort, occur upon the highest peaks of the Appalachian system, but the number of these is comparatively insignificant when compared with the rich and beautiful Alpine flora of the Canadian Rockies and the Cascades.

At the close of the glacial epoch the distribution of the plants was practically as at present, the most marked features being the eastern and western forest areas and the great open region of the great plains.

Part four deals with the floral regions as they now exist in North America. Probably most botanists will feel that the weakest feature of this account of the flora of North America is its lack of proportion. While the relatively uniform flora of the Atlantic half of the continent receives over 150 pages, the Rocky Mountain flora is dismissed with 23 pages, and the extraordinarily varied and interesting flora of the Pacific Coast with less than fifty. This no doubt is to be explained by the author's very intimate acquaintance with the flora of the Atlantic states, and his evidently very casual observations at first hand upon that of the western third of the continent; but he has not shown the best judgment in the selection of topics for discussion, dealing at great length with relatively very unimportant regions. Nearly as much space is given to a discussion of the pine-barren flora of the Atlantic Coast states as to the whole of the Pacific Coast from Alaska to Mexico. The multiplication of details in the discussion of the floras of small and unimportant areas, results in a general sense of confusion, and one is often at a loss to see the bearing of many of the detailed descriptions of local floras upon the larger problems. It is a pity that the abundant

materials had not been better digested, and much might just as well have been omitted. The contrast between the over-elaboration of many topics dealing with the Eastern flora, and the very casual treatment of the far more important and divergent conditions of the Rocky Mountain and Pacific region, is both striking and regrettable. However, with all these serious faults, the patient reader will be able to get a fairly comprehensive view of the extremely diverse features making up the flora of the North American continent.

With the last retreat of the great ice sheet, there moved into the territory thus uncovered plant migrants from various sources. Keeping close to the retreating ice sheet are the various strictly arctic or glacial types, and south of this northernmost flora is the extensive development of bog and tundra formations, which form so important a feature in the arctic and subarctic regions of Alaska, Canada and Greenland.

This northern area in America shows three sections, ranging from east to west. Greenland, separated from the mainland by the deep water of Baffin's Bay and Davis Strait, belongs really with Europe, its scanty flora being composed almost exclusively of European types like those of Scandinavia and Lapland. The middle region extending from Labrador to the Mackenzie River is marked by a larger preponderance of purely American types. Westward, including Alaska, the arctic flora is again characterized by a preponderance of Old World species. Out of 364 species of Western Arctic America no less than 320 occur in Northwestern Asia, many of them extending southward to the Altai and Himalaya Mountains. Of the 379 species belonging to the middle region 73 species are strictly American, the other 306 occur also in the arctic regions of the Old World.

The characteristic "tundras" are plains whose subsoil is permanently frozen, but whose surface soil is covered with a dense growth of mosses or lichens, among which grow in places dwarf Alders, Willows, Birches, and various ericaceous shrubs, *e. g.*, Cassiope, Andromeda, Vaccinium, Ledum, etc., as well as many herbaceous plants, some with showy flowers like the Iceland poppy. It is evident that the arctic flora is remarkably uniform throughout the whole northern hemisphere.

In connection with a study of the land plants some interesting features may be noted in regard to the arctic American Algæ. There is a remarkable difference between the Algæ of the

arctic regions of the Atlantic and the Pacific, many striking genera including the giant Kelps being quite unrepresented on the Atlantic side of the continent. Harshberger thinks that this points to these two regions as being distinct centers of development and distribution, and it may also show that some of the extraordinary Kelps of the Pacific Coast may be relatively recent developments.

South of the arctic zone is a sub-arctic forest zone, also of very similar composition throughout its whole extent from Labrador to Alaska. This forest is largely composed of Conifers, the predominant trees being White and Black Spruce, Balsam-Fir, Tamarack and Scrub pine.

With the Conifers are associated Aspens, Balsam Poplars, Willows, Alders and Birches. Swamps and peat bogs abound and in these as well as in the forest itself grow many attractive shrubs and herbaceous plants. Ericaceous shrubs are especially abundant, Rhododendron, Kalmia, Ledum, Vaccinium, etc., as well as wild Roses, species of Rubus and Ribes, etc. In the Sphagnum bogs, especially in the eastern portions, are found Pitcher plants, Sundew, and several beautiful Orchids. A considerable number of species, *e. g., Pyrola rotundifolia, Linnæa borealis, Cornus Suecica,* are identical with Old World species, and most of the genera, although not the species of trees, are the same.

To the southward of this uniform forest zone a greater divergence in the floras is noted, and within the United States the character of the vegetation changes radically as one proceeds from the Atlantic seaboard westward.

The whole of the eastern third of the United States may be said to comprise one great phytogeographical area, although of course there are certain regions where the flora has a more or less marked type of its own. Nowhere within this area are the mountains of sufficient elevation to form barriers against the ready migration of plants, and the whole region is one of abundant rainfall. The whole area being continuous, the result is a very uniform flora, when contrasted with the Pacific side of the continent. Many species of trees, *e. g.,* Elms, Oaks, Walnuts, Hickories, etc., occur throughout the range and the same is true of very many herbaceous plants. It is true that the number of species is much greater in some parts than others, owing to more favorable conditions of soil and temperature, but there are

no such radical differences within the area as those, for instance, between the Southern California desert and the Redwood belt of the coast region of the same state. The most important feature of this Eastern area is the great development of the dicotyledonous forest trees. Probably nowhere outside the tropics is to be found a richer forest flora, and the trees, both by their size and variety, constitute a truly magnificent forest. This forest reaches its finest development in the Southern Alleghenies of western North Carolina and in parts of the Ohio and Mississippi Valleys. Unlike the northern forest belt and the forests of most parts of Europe, this forest is composed of a great many species intermingled. It is stated by Harshberger that probably the richest forest vegetation in the north temperate zone is found in the lower Wabash Valley in Illinois, where one hundred and seven species of trees occur. In an area of less than a square mile in extent seventy-five species of trees were counted.

While many of these trees belong to European genera, *e. g.*, Poplar, Beech, Birch, Oak, Elm, Ash, etc., many genera are absent from the European forests. Such, for example, are the gums (Liquidambar and Nyssa), Magnolias, Tulip trees (Liriodendron), Hickories, Locusts (Gleditschia and Robinia), the Cypress (Taxodium), etc. Some of these trees reach really gigantic size, in regard to which Harshberger gives some striking figures. Thus a Red Oak is cited which was seven feet in diameter, with a height to the first branch of ninety-four feet, and a total height of one hundred and eighty-one feet. A White Oak and Bur-Oak of nearly equal size are mentioned, while a Cottonwood (*Populus monilifera*) was eight feet in diameter and one hundred and ninety feet in height. Thus it will be seen that some of the Eastern deciduous trees almost rival the Pacific Coast Conifers in size. Other giants of the eastern forest are the White Pine, the Sycamore and Tulip tree. With these are associated many shrubs and climbing plants, as well as a characteristic flora composed of herbaceous plants, usually flowering in the early spring before the leaves appear upon the trees.

In the Mississippi Valley the forest is almost exclusively composed of deciduous trees, but in the Appalachian forest there is a mixture of coniferous trees, especially Pines and Hemlocks, while in the north the proportion of these Conifers increases and at the same time many of the deciduous trees disappear, and the forest then consists of a comparatively small number of spe-

cies. In many parts of the northern states there is a preponderance of Beech and Maple, with a comparatively small number of other trees growing with them, but nowhere in the real forest area do we find the pure forests of Beech or Oak which are common in northern Europe.

In marked contrast with the preponderance of deciduous forests over most of the eastern states, are the areas known as Pine-barrens, characterized in certain districts by an almost pure forest of Pines, usually of a single species. Professor Harshberger gives a very exhaustive account of the Pine-barren flora, which he has evidently studied with great care.

At the north the prevalent Pine is *Pinus rigida*, with which are found associated some scrub oaks, Nyssa, Liquidambar, Sassafras and others, as well as a rich growth of showy ericaceous shrubs. The poor sandy soil is especially adapted to Ericaceæ, and Huckleberries, Azaleas, Kalmias, Rhododendrons, etc., are conspicuous features of the undergrowth. There are also extensive cranberry bogs where many beautiful Orchids occur, as well as Pitcher plants, Sundews and other interesting bog plants. In the coastal bogs of North Carolina grows the unique Venus's fly trap (Dionœa) and the long trumpets of the Southern Pitcher plants.

Over extensive regions of the Gulf states reaching into Texas are extensive forests of Pines, whose value as timber trees is only too well appreciated. The most important of these southern Pines is the long-leaf pine (*P. palustris*).

In the southern portion of the Atlantic states there is an infusion of tropical types, the most striking of which are the Palms, the common Palmetto reaching as far north as the coast regions of North Carolina. Certain genera of unmistakable tropical affinity reach even to the northern states. A conspicuous example is the Paw-paw (Asimina), a representative of the characteristic tropical family of Custard-apples. In the Gulf states there are many examples of plants of tropical affinities, including certain Orchids and members of the Pineapple family, of which the most familiar example is the Spanish moss, Tillandsia.

The southern part of Florida is very different in its flora from the northern portion, which is essentially the same as that of the other Gulf states. The southern extremity of Florida together with the Florida Keys really belongs to the West Indian floristic region. This is the only part of the United States which has a

real tropical flora. Along the coast there are extensive Mangrove swamps and the strand flora includes many West Indian types. Among the strand plants is the ubiquitous *Ipomœa pescaprœ* found on every tropic beach throughout the world. Another very widespread tropical plant occurring in the swamps along the shore is the stately fern *Acrostichum aureum*. This is also a common and conspicuous plant in the Nipa swamps of the East Indies.

A feature of southern Florida is the presence in the grassy lands of the everglades and in the dry sandy pine forests, of areas covered with hardwood trees. These wooded areas are known as "hammocks," and the vegetation, both the trees and lower growing plants, are mainly tropical types, for the most part West Indian species. There are many epiphytic Orchids and Bromeliads as well as tropical species of ferns, Palms, Figs, Mahogany and other West Indian types. In this region is found the only Cycad (*Zamia floridana*) occurring in the United States.

Proceeding westward, the rich forest vegetation of the Atlantic Gulf states and the eastern Mississippi Valley begins to thin out with the falling off in the rainfall toward the interior. In western Michigan, Indiana and Illinois there are already encountered open prairies, and the forest is much less luxuriant. Open groves of Oaks, Hickories and Walnuts, the so-called "oak openings," are characteristic formations of this region. Further west these disappear, and the whole country forms a continuous open prairie. How far the formation of the prairie is due to climatic causes, *i. e.*, insufficient rain and cutting winds, and how much is due to compact soil (loess) which often underlies them, and which seems unfavorable for tree growth, is not quite clear; but throughout the prairie region trees are practically confined to the beds of the streams and the sheltered gullies between the hills.

Still further westward the prairie insensibly merges into the semi-arid plains, which end abruptly at the foot of the great barrier of the Rocky Mountains.

Compared with the eastern third of the continent the flora of the great central plains is scanty. Grasses predominate, but there are a good many showy flowers which adorn the prairie in the spring and summer. Conspicuous among these are numerous Compositæ, Rosin Weed, Rudbeckia, Sunflowers, Asters, Golden-rods, and many others.

The western third of the continent is much more varied in its topography than the Atlantic side, and shows a correspondingly greater richness and diversity in its flora, since the climatic differences, due to the extremely varied topography, are much greater than is the case in the eastern states.

Rising abruptly from the plains, the Rocky Mountains form the beginning of the great complex of mountains and deserts that stretches to the Pacific Coast. Unlike the worndown Appalachian system, the western mountains are extremely rugged, and their much greater elevation, rising above the level of perpetual snow, permits of a true Alpine flora. The region bordering on the great plains is arid and semi-arid, and has a pronounced continental climate, with great extremes of heat and cold and a scanty rainfall.

The lower elevations are mostly destitute of forests except along the water courses and in sheltered cañons. Higher up the precipitation increases, and at elevations of from five to ten thousand feet a fairly heavy forest is found, in many places composed mainly of coniferous trees. Of these the most important are the Rocky Mountain Yellow-Pine, the Douglas Fir, the Lodge-pole Pine and Engelmann Spruce. At the lower elevations where trees are found they are mostly of Eastern species, some of which, like the White Elm and Cottonwood, are found sparingly as far west as the base of the Rockies.

For the most part, however, the Rocky Mountain flora is allied to that of the Pacific Coast and the arid southwestern region whose plants are mainly of Mexican origin. A marked feature of the eastern Rocky Mountains is the formation of beautiful glacial parks, which are especially well developed in Colorado. The floors of these parks are covered with a rich carpet of grasses and showy flowers, and the mountainsides support a fairly dense growth of Pines and Spruces with a few deciduous trees like the Aspens and Birches. To the west of the main range of the Rockies lies the elevated arid plateau of the Great Basin, including most of Nevada, Utah, northern Arizona and New Mexico.

This region especially the southwestern portion is one of the most interesting botanical areas of the continent. It is continuous with the Mexican plateau which seems to have been the center of development for the many interesting and peculiar xerophytic types which are so remarkably developed in this region. Among these the Cacti take first place, an almost exclusively American

family. Other striking and characteristic forms are Yucca, Agave, Mesquit (Prosopis), the Creosote-bush (Larrea), the Ocotilla (Fouquiera) and several other characteristic American genera. This peculiar xerophytic flora is especially well developed in southern Arizona, and visitors to Tucson have an excellent opportunity of seeing it in great perfection.

In the northern part of the Great Basin region the Cacti are almost entirely absent and the desolate country is covered by Sagebrush, Greasewood, and many scrubby Compositæ, producing a landscape that is monotonous in the extreme.

In the northwestern area, through Canada and the northern tier of states, the true desert is practically absent, and the mountains are covered with a heavy growth of timber mostly made up of western Conifers. The other plants are largely subarctic and northern types, but mingled with these are a good many western genera, such as Pentstemon, Fritillaria, Gilia, and others.

On the western slope different conditions prevail and the ameliorating effects of the west winds from the Pacific make themselves felt. This is, however, not fully seen until the last of the mountain ranges is reached, the great Cordillera, which stretches practically without a break from Alaska to Patagonia. It is this great barrier, averaging in California some ten thousand feet in height, that largely determines the character of the Pacific Coast climate. Protected entirely from the sudden changes of the great interior continental area, with prevailing westerly winds from the vast Pacific whose temperature scarcely changes from one year's end to the other, the whole western coast enjoys an extraordinarily equable and temperate climate.

On the Pacific Coast topography is a far more important factor than latitude in determining climate. Close to the coast the climate is uniformly cool, and seldom either hot or cold. San Francisco in latitude 37°, with an annual mean temperature of 56° F., shows a range of scarcely ten degrees between the hottest and the coldest months. Sitka, 20° farther north, has a winter temperature about the same as that of New York City. Naturally the character of the climate has affected the vegetation profoundly, and with the great differences in elevation and precipitation found along the Pacific Coast, the variety of the vegetation is much greater than in Atlantic North America.

The coast of Alaska, as far north as about sixty degrees, has a winter temperature about the same as that of the middle

Atlantic states, but with a very heavy precipitation, so that it supports an extremely dense forest of large coniferous trees, of which the Tideland or Sitka Spruce (*Picea Sitchensis*) and the Hemlock (*Tsuga Mertensiana*) are the predominant trees. There is an impenetrable jungle of undershrubs and herbaceous plants of almost tropical luxuriance.

Further south the Sitka Spruce is largely replaced by the Douglas Fir, the characteristic tree of the coast region about Puget Sound and northern Oregon. This tree rivals the California Redwoods in height though not in bulk. At the lower levels of the coast in Washington and northern Oregon the forest over large areas is composed almost exclusively of this species, but back from the coast at the higher levels this is to considerable extent replaced by Pines, Firs and Hemlocks. This change in the forest is very clearly shown on the slopes of Mt. Rainier.

The undergrowth of this northern forest is very much like that in Alaska. Among the characteristic species are *Rubus Nutkanus, Rubus speciosus,* several species of Elder, the Vine-leaved Maple (*Acer circinnatum*) and the Devil's-club (*Echinopanax horridum*). At the lower levels Alders and Poplars of large size are common along the streams, and with these are found the Big-leaved Maple (*Acer macrophyllum*). Where the forest has been destroyed, especially in burnt-over areas, the ground is covered in mid-summer with a sheet of pink flowers of the Fire-weed (*Epilobium angustifolium*), Bracken ferns of gigantic size and the striking Aroid, *Lysichiton Kamtchatcense,* give a tropical aspect to the dense undergrowth. Most of the herbaceous plants are northern types, Linnæa, Oxalis, Smilacina, Clintonia, *Cornus canadensis,* etc.

At an elevation of about five thousand feet there begins an Alpine flora which is especially well developed on the higher snow-capped mountains of the Cascades and the Canadian Rockies. On Mt. Rainier, where the line of perpetual snow descends to but little over six thousand feet, the close turf, left uncovered for a couple of months after mid-summer, is covered with masses of brilliant flowers of great variety and beauty. Among the most striking of these are two heathlike plants, *Bryanthus* and *Phyllodice,* a very large and beautiful Erythronium (*E. montanum*), a splendid crimson Castilleia, bright blue Lupins, Veronica, white Valerian, several species of Pedicularis, Anemone, Mimulus, Gentian, and many others.

Passing southward from Oregon into California, the outer coast mountains from the Oregon line to Santa Cruz, some fifty miles south of San Francisco, are dominated by the Redwood (*Sequoia sempervirens*), the tallest of all trees, which reaches its greatest development in the northern coast counties of Mendocino and Humboldt. These giant trees occur only in the narrow belt within reach of the heavy summer fogs which prevail along the coast. In most parts of the Redwood belt there is a greater or less mixture of other trees, *e. g.*, Madroño (*Arbutus Menziesii*), the Tan bark Oak (*Quercus densiflora*) the Douglas Fir, wild Nutmeg (*Torreya californica*), the wild Bay tree (*Umbellularia*) and the big-leaved Maple.

South of San Francisco there is a rapid diminution in the rainfall and the Redwoods gradually disappear and are replaced by more xerophytic types. Some of these, like the Monterey-Pine and Cypress and the Torrey Pine of Southern California, are of very restricted range, forming scattered forests along the coast, and extending down to the very edge of the ocean.

Many of the plants of the Redwood belt are northern types which thrive in the cool forests of the outer coast range. Representing familiar northern and southern genera may be mentioned species of violets, Trillium, Clintonia, Oxalis, Smilacina, Asarum, Aquilegia, Delphinium.

Of characteristic shrubs of this region there may be cited species of Ribes, Ceanothus, Gaultheria, Rhododendron, Azalea, Vaccinium, Rubus and Arctostaphylos. In middle California these northern plants follow the shady cañons almost to the level of the valleys, where they mingle more or less with the valley flora which is comprised mostly of strictly Western types.

In many places along the Coast there is an extensive development of sand dunes, which support a very rich and interesting flora. Characteristic plants of the sand dunes are species of Abronia, Lupinus, Erigeron, Œnothera, Eschscholtzia, Fragaria, Mesembryanthemum.

In middle California three ranges of mountains parallel with the coast are found. The Outer Coast-range skirts the ocean, and a break in this at San Francisco forms the Golden Gate, opening into the Bay of San Francisco, which receives the united waters of the two rivers draining the great central valley. The latter is separated from several smaller valleys to the west, the most important being the Santa Clara Valley, by the inner Coast

Range which farther south joins the outer Coast Range. The rainfall in these valleys shut off from the ocean by the intervening mountains is relatively small, and the floors of the valleys are usually open plains with only a scattered growth of spreading trees, mostly Oaks. In the great central valley much of the land is too dry to support any tree growth and there are extensive grassy plains recalling the prairies of the Middle West.

The open valleys and the foothills are the home of an extraordinary variety of beautiful flowers, which in spring spread a gorgeous carpet over the landscape. These flowers are largely annuals which start into growth at the first autumn rains, and flower in the early spring, ripening their seeds and dying with the oncoming of the summer drought. There are also many bulbous plants, some of great beauty like the exquisite Mariposa lilies and Brodiæas. While some of these valley plants like the California Buttercup and species of Clover are allied to Eastern types, the great majority are western or belong to western and southwestern genera. Representative genera are Lupinus, Orthocarpus, Eschscholtzia, Nemophila, Gilia, Platystemon, Godetia, Clarkia, and an extraordinary variety of showy Compositæ.

A characteristic feature of the hillsides and dry mountain slopes is the "Chaparral," a dense and often impenetrable growth of shrubs of many kinds, scrub Oaks, Chinquapin, Poison-oak (Rhus), Buckeye, Ceanothus, Ribes, Heteromeles, Adenostoma. Most of these are evergreen, but some like the Buckeye and Poison-oak, are deciduous.

To the east of the great valley lies the Sierra Nevada, rising to an altitude of nearly fifteen thousand feet with a flora of great variety and beauty. The lower slopes covered with chaparral and with scattered Oaks and Digger Pines (*P. Sabiniana*) give way at higher altitudes to perhaps the finest coniferous forests in the world. At an altitude of about four to six thousand feet is the great forest belt where grow the scattered groves of the Giant Sequoia, associated with hardly less imposing Sugar Pines, Yellow Pines, Firs and Incense Cedar. As an undergrowth there are found Dogwoods, Oaks, Aspens, and many beautiful flowering shrubs like the Azaleas, Ceanothus, Philadelphus. The low meadows near the water courses are full of showy flowers, Lupins, Castilleia, Lilies, Veratrum, Monk's-hood, Larkspur, and many others.

In the chaparral may sometimes be seen the magnificent Washington-lily and the stately Humboldt-lily, while under the shade of the great Conifers the vivid crimson Snow-plant (Sarcodes) may often be found.

Southern California is largely a desert region, the transverse Tehachapi range of mountains shutting it off from the great central valley to the north. The Mojave desert, south of the Tehachapi, is an arid plateau whose scanty vegetation is of a marked xerophytic type. Cacti are abundant and the most striking plants are the tree Yuccas (*Y. arborescens*). Other species of Yucca with magnificent panicles of white flowers also occur, flowering in the late spring and early summer. Farther south there are rich valleys opening toward the sea, and less arid than the tableland to the north, and the Colorado desert to the southeast. The latter region, which includes Death Valley, is a desert of the most pronounced type, some of it lying below sea level, and extremely hot and dry. Opening into the Colorado desert, however, there are small cañons with permanent streams coming down from the lofty mountains, and supporting a more or less mesophytic growth of Cottonwoods, Sycamores and Willows, and in some of the cañons there are imposing groves of the stately Washington Palm (*Washingtonia filifera*). This southern region is really part of the great Sonoran region of Mexico and its vegetation is essentially the same.

The remarkable range in conditions often within very short distances, *e. g.*, the eastern and western slopes of the Coast ranges, results in an extraordinary variation in the vegetation within a relatively small distance, and perhaps no equal area in the world, outside the tropics, can show a greater number of species than California. Moreover, a very large number of these species are endemic and there are also very many peculiar genera. Some of the genera are characterized by a great number of species. Thus the genus Ribes (see Harshberger, p. 273) is credited with forty species against thirteen for the whole region covered by Britton and Brown's Manual. Other large genera are Calochortus, Orthocarpus, Pentstemon, Lupinus, Trifolium, Gilia.

Professor L. R. Abrams has kindly furnished the writer with some data showing the remarkable endemism of many California genera. Of the forty known species of Ceanothus thirty occur in California, and twenty-five of these are endemic. Sidalcea with a total of nineteen species is represented in California by

seventeen, of which thirteen are peculiar. California has some sixty species of Lupinus, out of a total of about one hundred described species, and of these forty-five are endemic. More than half of the known species of Gilia occur in California and more than half of these (thirty-four out of fifty-seven) are endemic. Many other cases could be cited but these will suffice to show the extraordinary degree of endemism exhibited by the flora of California.

The remarkable development of coniferous trees in California is of course famous. Within the state are nearly twice as many species of coniferous trees as in the whole region east of the Rocky Mountains. Moreover, a considerable number of these species are quite peculiar to the state, and often of very limited range, as for example the Big Tree and the Monterey Pine and Cypress.

While the flora of Oregon and Washington has much in common with the Rocky Mountain region, and even with the Atlantic states, the northern elements are much less prominent in California, although owing to the southward trend of the mountains, many northern types reach far southward, especially in the cool, moist forests of the outer Coast range, where such northern genera as Trillium, Oxalis, etc., are abundant. There is a certain number of types which seem to be of Asiatic affinity, *e. g.*, Fritillaria, Lysichiton, and Tan-bark Oak, but in the drier regions the plants are for the most part allied to Mexican and South American forms. Of the latter there are certain species belonging to Chili and Argentina which also occur in California, but are absent from the intermediate territory.

An interesting feature of the Pacific flora is the occurrence of certain genera belonging to the Mediterranean region, *e. g.*, Arbutus, Cupressus, Lavatera, and there are also a few Old World Ferns and Liverworts which are absent from Eastern North America. Of the latter we may cite *Woodwardia radicans, Equisetum telmateia, Targionia hypophylla.* The survival upon the Pacific Coast of these latter types, which are probably old ones, is presumably due to climatic reasons, and perhaps this explanation may apply to the occurrence of the phænogamic genera as well, a case comparable to the many correspondences between the flora of eastern Asia and that of Atlantic North America.

Only a small part of North America lies within the tropics,

and much of this is so elevated that the flora is not really a tropical one. The whole of the interior of Mexico is an elevated tableland, with a flora closely resembling that of the southern and southwestern United States.

The eastern coast of Mexico, together with Central America and Panama, possesses a tropical flora belonging with that of South America. In this region Palms, Aroids, Cannaceæ, Bombacæeæ, arborescent Leguminosæ, and other tropical types abound, and there is a very rich development of epiphytic Orchids and Bromeliads.

The extreme southern part of Florida, as we have seen, is the only part of the United States which properly belongs to this tropical area, although a good many Southern types extend much farther north than this. Such Southern types are the Palmettos, Tillandsia, and other Gulf-state species.

While the eastern coast of Mexico has a humid hot climate with the typical tropical flora, the western coast is extremely arid with a scanty xerophytic vegetation.

The West Indian region is treated by Dr. Harshberger as a distinct province. There is developed here a rich and interesting flora, allied, as might be expected, to that of the American mainland, but comprising many peculiar species. The larger islands are very mountainous and great differences in the vegetation conditioned by topography may occur within very short distances. This is well illustrated in Jamaica, where the vegetation on the north and south sides of the island is very different, although only forty miles apart. This difference is caused by the presence of a range of mountains over seven thousand feet high in the middle of the island. Jamaica is remarkable for the great development of Ferns, being perhaps the richest area of its size in the world. It is said that some five hundred species occur in the island, which has an area of only about four thousand square miles.

Dr. Harshberger's handsome volume is illustrated with a profusion of excellent figures, many of them original photographs, which add greatly to the value of the book, which must remain for a long time to come the standard work on the distribution of the plants of North America.

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